Modelling the effects of odours and spying parasitoids on fruit fly population dynamics

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Abstract

Chemical information mediates many species interactions. This has been mostly studied at the level of individual organisms. The central question in this thesis is how intraspecific chemical information conveyance and exploitation thereof by a natural enemy affects the spatial population dynamics of a species. To answer this question, I developed a spatio-temporal model where both host and parasitoid can respond to infochemicals. The model system consists of the fruit fly *Drosophila melanogaster*, and its natural enemy, the larval parasitoid *Leptopilina heterotoma*. *D. melanogaster* uses its aggregation pheromone in combination with odours from fermenting fruits to localise suitable resources for reproduction. *L. heterotoma* uses these same odours to localise its host. For *D. melanogaster*, aggregation on a resource can be beneficial when a population is small and has to overcome negative effects associated with low population densities. Such negative effects, known as the Allee effect, can for instance be caused by difficulties in resource exploitation or in finding a mate. Aggregation also involves costs. Individuals within an aggregation frequently experience more severe competition for food, space and mates than they would experience when being on their own. By means of simulations, the net effect of both costs and benefits is studied. Furthermore, the study addressed which behavioural decisions of the fruit flies enhance the ability to find – and distinguish between – odour sources that differ in their suitability for reproduction.

On the individual level, this research showed that, like real fruit flies, the modelled fruit flies need to have a preference for the presence of both aggregation pheromone and food odours, over food odours alone, to be able to distinguish between the two types of odour sources. The results show that this stronger preference does not have to be innate. As long as fruit flies are able to remember and adjust their current preference based on the odour concentrations that they perceive, more fruit flies find the more attractive odour source.

On a population level, this thesis shows that the use of infochemicals by *D. melanogaster* affects its population dynamics. In the absence of its natural enemy, and when the *Drosophila* population is small, the use of food odours and aggregation pheromone has a positive effect on population growth and enhances the fruit fly's colonization ability. When the population becomes larger, however, the negative effects of larval competition are stronger than the positive effects of reduced mortality due to the Allee effect. The ability to use chemical information is crucial to colonize an area from the boundaries. A fruit fly population without this trait could not colonize the area and went extinct. When parasitoids can use chemical information, parasitism rates are higher, resulting in a slower population growth of their host. No difference was recorded in fruit fly population size and in larval mortality due to parasitism, when parasitoids exploited the aggregation pheromone of the fruit fly adults as compared with the simulations where the parasitoids could only respond to chemicals emitted by the host habitat. In contrast, the use of chemical information by the host enhanced its population growth and enabled it to survive, even at higher parasitoid densities. This research showed that mortality when the population was small had a greater impact on *Drosophila* population size than mortality due to competition or parasitism. As food patches are not always abundant in nature, the reproductive success of fruit flies is more determined by their opportunities of producing clutches (i.e. locating patches) than by preventing over-aggregation or parasitism. As a result, the use of chemical information has a net positive effect on fruit fly population dynamics, despite the fact that *L. heterotoma* is able to exploit it.

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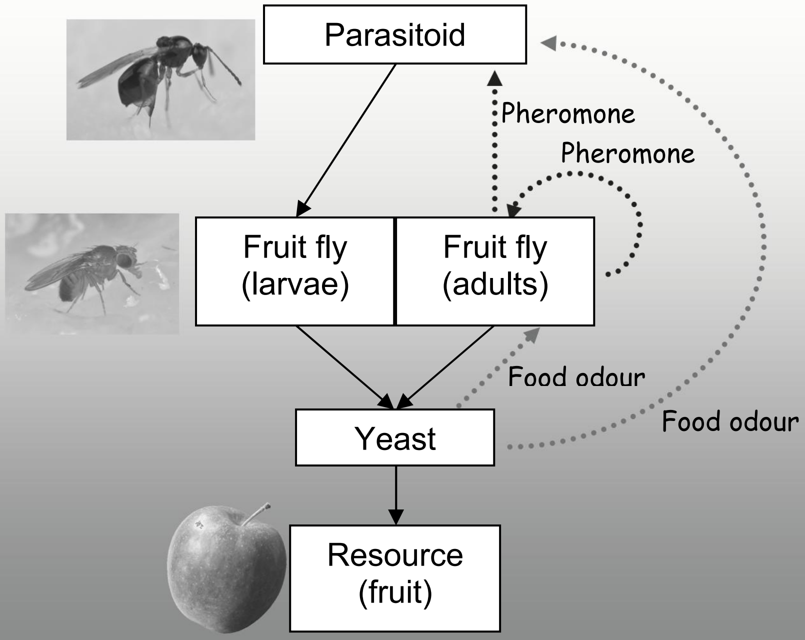
Abstract

Chapter 1



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General introduction

Modelling the effects of odours and spying parasitoids on fruit fly population dynamics

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1.1 The role of chemical information in a food web

Chemical information conveyance plays an important role in the biology of many species ranging from microbes to mammals (Bell and Cardé, 1984; Wyatt, 2004; Kats and Dill, 1998; Dicke and Takken, 2006; Vos et al., 2006). Animals are well equipped to gather information about their environment, and they are assumed to use the information to adjust their behaviour so that it contributes to the maximization of their fitness (Krebs and Davies, 1997). The chemical substances involved are termed infochemicals (Dicke and Sabelis, 1988). Infochemicals can provide information on the availability of food or mates, as well as the presence of competitors or natural enemies; thus, they can affect interactions in an ecological food web (Box 1). Once an infochemical is emitted, in principle any organism can exploit its information. The interactions between species in an ecosystem that are influenced by information can be represented in a so-called information web that is more complex than the underlying food web (Dicke and Baldwin, 2010). Infochemicals affect the dispersal and distribution of organisms, the distribution of competitor species and natural enemies, and consequently, the population dynamics of many, if not all, food web species. Yet, the study of chemical information conveyance has been mostly restricted to studies at the level of individual organisms and the identification of chemical substances that convey the information. The central question in this thesis is how chemical information conveyance affects spatial population dynamics of species and the interactions between species within a food web. I address this question by using a modelling approach.

1.2 Aggregation

In an aggregated distribution, the individuals are more close to each other than in a random distribution. Aggregation can arise when individuals tend to be attracted to particular parts of the environment or when individuals respond behaviourally to the presence of conspecifics and actively search for each other. Forming aggregations is a general phenomenon in the animal kingdom (Parrish and Edelstein-Keshet, 1999). It can especially be beneficial when a population is small and has to overcome negative effects associated with low population densities. Such negative effects, known as the Allee effect (Allee, 1931), or a reduced per capita growth rate at low population densities, can for instance occur due to difficulties in finding a mate or difficulties in resource exploitation (Wertheim et al., 2005). Protection from predators is also viewed as an important selective advantage of group membership resulting from aggregation (Parrish and Edelstein-Keshet, 1999, Wertheim et al., 2005). For instance, when the group size is larger than the number of hosts or prey that a single natural enemy can attack, an individual has a diluted risk of attack. In some cases, a large group can defend itself against a predator. However, aggregation also involves costs, because individuals within an aggregation frequently experience more severe competition for food, space and mates than they would experience when being on their own. Moreover, within a bigger group a pathogen can be more easily transmitted than between individuals in a small group. Also, the group as a whole can be more conspicuous to natural enemies (Parrish and Edelstein-Keshet, 1999).

Box 1 To exploit and to be exploited – feeding relations and chemical communication shape the interactions in a food web.

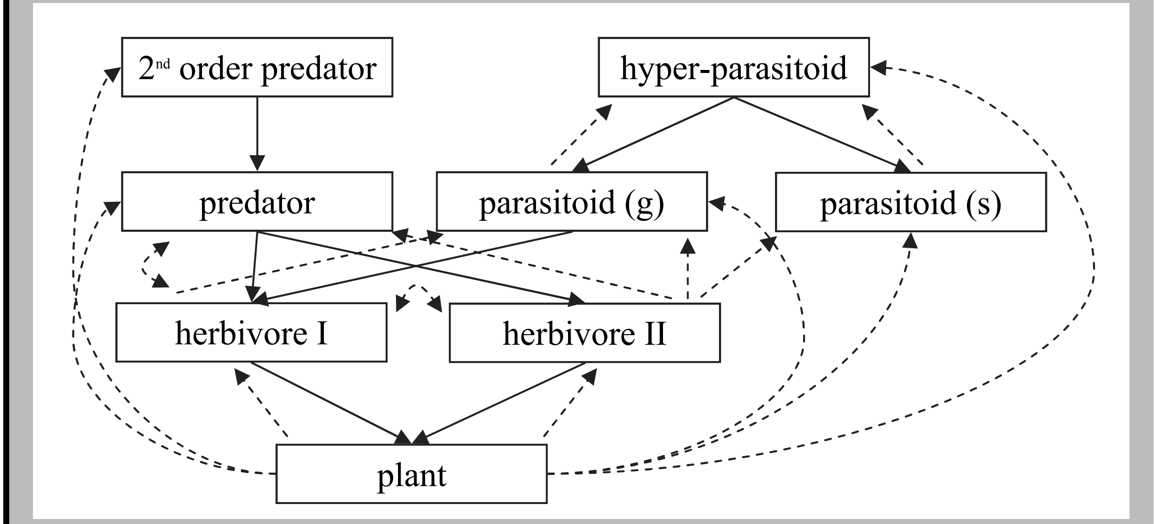

Figure I An example of a food web overlaid by an information web. Solid arrows depict feeding relations (the arrow points to what is consumed), dotted arrows depict competition, dashed arrows depict chemical information. Chemical information can link consecutive trophic levels but also skip trophic levels and affect the decisions of organism two (or more) trophic levels higher. In this graph, parasitoid (g) is a generalist that parasitizes multiple host species, while parasitoid (s) is a specialist that only attacks one host species.

Food chain

A food chain represents a connected number of species; at each level, the species eats a species of a lower level, and is eaten by a species of the next level. The number of steps an organism is from the start of the chain is a measure of its trophic level. Most food chains consist of three or four trophic levels (but for insects often more than 4 trophic levels). Green plants form the first trophic level, herbivores form the second trophic level, while carnivores and top carnivores form the third and the fourth trophic levels, respectively. Another sequence in a food chain is plant, herbivore, parasite of herbivore (parasitoid) and a parasitoid of the parasitoid (hyperparasitoid).

Food web

Food chains intertwine into a food web because most consumers feed on multiple species and in turn, are fed upon by multiple other species. In addition, many species feed on more than one trophic level (for instance on plants and herbivores). Therefore, even a simplified food web can show a complicated network of trophic relationships.

Information web

Organisms invariably emit chemical compounds, either deliberately through communication with conspecifics, or involuntarily as a side-effect of their activities. This chemical information can affect interactions in a food web at various trophic levels. Infochemicals can provide information on the availability of food or mates, as well as the presence of competitors or natural enemies. Once an infochemical is emitted, in principle any organism can exploit the information. As a result, the information web, based on infochemicals, can be even more complex than the underlying food web.

Animal aggregations can arise when individuals actively search for each other. One important mechanism that can lead to the formation of aggregations is communication among individuals. This communication can, for instance, be auditory, visual or chemical. Each of these communication modes has its own advantages and disadvantages, such as speed, reach, directionality and specificity. Many insects use chemical information to form aggregations. Specific infochemicals involved here are the so-called aggregation pheromones, chemical compounds that cause aggregative behaviour in conspecifics of both sexes or in the same sex as the emitter (Wertheim et al. 2005). A review by Wertheim et al. (2005) showed that among non-social arthropods alone, over 300 species have been reported to use aggregation pheromones.

Aggregation can also play an important role when a species is colonizing or re-colonizing an area. If a species arrives in an unoccupied area it must be able to feed and to produce offspring. Forming aggregations can then facilitate resource exploitation or finding a mate (Raffa, 2001).

1.3 Chemically mediated parasitoid-host interactions

Parasitoids are common natural enemies of insects (Godfray, 1994). Adult female parasitoids lay one or more eggs in or close to the body of a host, which is usually an egg or an immature stage of another insect species. This host is then consumed by the developing parasitoid larva, which results in the death of the host. The fitness (i.e. the lifetime reproductive success) of a parasitoid depends on its ability to find and attack hosts; as a consequence parasitoids are under strong natural selection to develop efficient host search and attack strategies. The ability to find a host may be enhanced by spying on the chemical information that the parasitoids' host species uses for communication with conspecifics (Wiskerke et al., 1993; Hedlund et al., 1996; Wyatt, 2004; Fatouros et al., 2005a). The compounds used to convey information intraspecifically can provide searching parasitoids with information on where to find their hosts. However, chemical information emitted by the host is usually not well detectable over long distances, as the host is under strong natural selection to be inconspicuous for its natural enemies. Chemicals released from the host's habitat, such as yeast odours, are often better detectable over long distances; yet, the information that they convey is not very reliable, because the presence of a suitable habitat for the host does not necessarily imply the presence of the host. This is known as the reliability-detectability problem (Vet and Dicke, 1992). For the parasitoid, one way to solve this problem is to exploit the chemicals that the hosts emit to communicate with conspecifics, such as sex pheromones or aggregation pheromones (Vet and Dicke, 1992; Hedlund et al., 1996; Dicke et al., 1994; Fatouros et al., 2008). The chemical information exploited by a parasitoid may be from a different life stage than the stage under attack (infochemical detour), as long as it can provide reliable information on the presence of the host stage under attack (Wiskerke et al., 1993; Noldus, 1989; Dicke et al., 1994; Vet and Dicke, 1992). For instance, egg parasitoids can use pheromones of the adult stage of their host (Noldus et al., 1991; Fatouros et al., 2005a).

Chemical information conveyance can also occur between plants and parasitoids or predators. Plants can produce and release volatile compounds in response to herbivore feeding, which are attractive to parasitoids or predators of the attacking herbivores (Dicke et al., 1990; De Moraes et al., 1998; Turlings and Wäckers, 2004; Tentelier and Fauvergue, 2007). The role of herbivore-induced plant volatiles in mediating interactions between plants, herbivores and their natural enemies has received considerable attention over many years (Price et al., 1980; Turlings et al, 1990; Heil, 2008; Poelman et al., 2008). Plants may benefit from herbivore-induced volatiles through reduced damage from the herbivores when the volatiles attract a predator or parasitoid of the herbivores (Vet and Dicke, 1992; van Loon et al., 2000; Fatouros et al, 2005b). The induced plant volatile blends may provide specific information to parasitoids about the identity of the herbivore, such as the species (De Moraes et al., 1998; Dicke, 1999), developmental stage (Takabayashi et al., 1995), or parasitization status (Fatouros et al., 2005b).

1.4 Modelling approach

Models for host-parasitoid systems have been fruitful for many experimental and theoretical investigations and have provided ample knowledge on parasitoid population dynamics (Godfray, 1994; Hassell, 2000; Wajnberg et al., 2008). Traditionally, there are two distinct starting points in exploring population dynamics in parasitoid-host systems. The basic assumption in Lotka-Volterra models (Lotka 1925; Volterra 1931) is that the generations of the interacting populations are overlapping and that birth and death processes are continuous. This model was developed to describe predator-prey interactions. Entomologists initiated a separate modelling tradition, in which the populations have distinct and synchronized generations (Thompson, 1930; Nicholson, 1933; Varley, 1947). For a long time the spatial aspects of parasitoid-host systems have received little or no attention in such models. However, work by Tilman and Kareiva (1997), and Turchin (1998) shows that spatial aspects can be very important. Modelling studies that include spatial effects have mainly focused on optimizing searching strategies (foraging behaviour) in environments where resources are heterogeneously distributed (Charnov, 1976; Haccou et al., 1991; Bukovinszky et al., 2007). Other modelling studies on population dynamics in parasitoid-host systems focus on temporal stability or on spatio-temporal patterns (Ives, 1992; Hirzel et al., 2007; Nguyen-Huu, et al., 2006; Pearce et al., 2007; Schofield et al., 2005). There are few studies that model the effect of chemical information on spatio-temporal parasitoid-host dynamics. Puente et al. (2008), Pearce et al. (2007) and Schofield et al. (2002) studied the effects of chemical information; however, in these studies only the parasitoid responds to chemical information, i.e. herbivore-induced plant volatiles, whereas the response of the herbivorous host to chemical information is not included. In this thesis, I develop a spatio-temporal model that describes the within-generation movement and interaction of parasitoids and hosts in a two-dimensional spatial domain, where the movement of both host and parasitoid are affected by chemicals emitted by the host and the host's habitat.

While not a replacement for field studies, computer simulation models can be used to predict what the effect of the use of chemical information is on population dynamics in parasitoid-host systems. They allow us to study the effect of changing variables that are difficult to estimate by direct experiments, while at the same time other factors can be kept constant. In this study, I artificially establish different responses (or no response at all) to chemical information by the host and its parasitoid. One purpose of this modelling study is to examine the effects of the use of an aggregation pheromone by the host on the population dynamics of the host, both in the absence of parasitoids, and in the presence of parasitoids that are capable of exploiting their communication system.

1.5 The model system

In this thesis, I explore odour-mediated interactions between a parasitoid species and a host species, and the consequences on the long term population dynamics of the host. As a model system I use the fruit fly *Drosophila melanogaster* and its natural enemy, the larval parasitoid *Leptopilina heterotoma*. Both *D. melanogaster* and *L. heterotoma* respond to odours of the microhabitat of *D. melanogaster*, and to the aggregation pheromone produced by *D. melanogaster*. There is ample knowledge on the response of *D. melanogaster* and *L. heterotoma* to these odours (e.g., Dicke et al. 1984; Bartelt et al., 1985; Wertheim et al., 2006; Wiskerke et al., 1993; Hedlund et al., 1996; Wertheim, 2001, Wertheim et al., 2003).

Drosophila melanogaster

Picture: Hans Smid,
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Drosophila melanogaster

The fruit fly *D. melanogaster* feeds and breeds on decaying plant material, mainly fermenting fruits. In their natural environment these substrates are distributed unevenly. Chemical attraction to odours from the food substrate and the fruit flies' own aggregation pheromone are instrumental in the localization of these substrates (Hutner et al., 1937; West, 1961; Bartelt et al., 1985; Wertheim et al., 2006). The aggregation pheromone is produced by the male fruit flies and transferred to the females during copulation. The pheromone is released into the environment by the females when they lay their eggs and it induces aggregated oviposition by females as well as attraction of males (Wertheim et al., 2006).

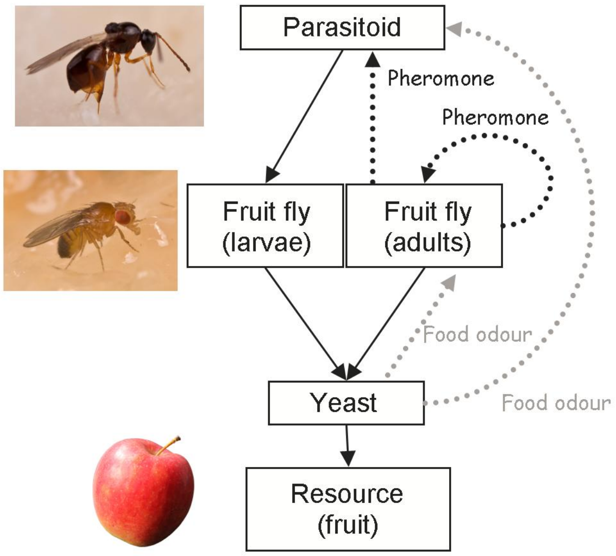


Figure 1 The food web and information web interactions in the *Drosophila-Leptopilina* system. The yeasts on the fermenting fruit produce a mixture of odours. These food odours attract adult fruit flies to the resource (the fermenting fruit). Adult males and mated females release an aggregation pheromone at the resource. This attracts conspecific adults to the resource. The parasitoid spies on the communication of the adult fruit flies. It uses both food odours and the aggregation pheromone of the adult fruit flies to find its host, the larvae of the fruit fly.

Both the adult fruit flies and their larvae feed on yeasts that live on the substrates. Larval survival of *D. melanogaster* is positively affected by adult aggregation, because adults enhance the suitability of the resource for the juveniles. Adults, especially females, carry along a diversity of yeasts and inoculate the resource with these yeasts during their presence (Morais et al., 1995). This increases the amount of food that is available for the larvae. At the same time, this increase in yeast also reduces fungal growth (Wertheim et al., 2002; Rohlfs and Hoffmeister, 2005). As fungi and yeast compete for resources in fruit, any process that favours one of the competitors (in this case the yeast) could result in a shift in the competitive interaction. This positively affects larval survival, because strong fungal growth can cause a high mortality in fruit fly larvae (Rohlfs et al., 2005, Rohlfs, 2006). Furthermore, the larvae of *D. melanogaster* themselves are also able to suppress fungal growth by disrupting the hyphae of the fungus. Larger groups of larvae are more successful at this than smaller groups or a single larva (Rohlfs et al., 2005, Rohlfs, 2008). The local interaction with the fungi gives rise to an Allee effect. However, there can also be costs involved with aggregation. With an increasing larval density on the resource, the chance that all larvae complete their development before the resource is depleted decreases. This then results in high mortality due to competition.

Leptopilina heterotoma

Picture: Hans Smid, Bugsinthepicture.com

Leptopilina heterotoma

L. heterotoma is a solitary larval endoparasitoid. An endoparasitoid grows inside the host while the host continues its own development. Solitary parasitoids only produce one offspring per host. *L. heterotoma* is a generalist that attacks a variety of *Drosophila* species inhabiting a variety of ephemeral substrates (Janssen et al., 1988). *L. heterotoma* parasitoids exploit the aggregation pheromone of the adult fruit flies to localize their hosts, the larvae of the fruit fly. *L. heterotoma* has an innate response to the aggregation pheromone, cis-vaccenyl acetate, produced by *D. melanogaster* and some other *Drosophila* species (Hedlund et al., 1996). *L. heterotoma* is able to learn to respond to odours that are produced by the different host habitats as well, after having encountered them in association with oviposition in host larvae (Dicke et al., 1984; Papaj and Vet, 1990; Vet and Groenewold, 1990; Hedlund et al., 1996). After an oviposition experience *L. heterotoma* can even learn to respond to odours that are not naturally emitted by its host or the habitat of its host (Vet and Groenewold, 1990).

The aggregation pheromone of *D. melanogaster* is a relatively reliable cue for *L. heterotoma*, because it is mainly emitted by recently mated females and it is persistent for several days (Bartelt et al, 1985), bridging the time-gap between oviposition by the fruit flies and the larval stage that is suitable for parasitoid oviposition (Wiskerke et al, 1993). Additionally, the concentration of aggregation pheromone gives quantitative information, both directly and indirectly: a high concentration is most likely released by more female fruit flies, while on the other hand higher concentrations of aggregation pheromone concentrations also attract more new fruit flies (Wertheim et al., 2006). The attraction of *L. heterotoma* is also positively dose-dependent (Wertheim et al., 2003). Furthermore, the parasitism rate is higher on substrates that emit aggregation pheromone (Wertheim et al., 2003).

1.6 Research objectives and outline of the thesis

In this study, I focus on two main questions. At a general level: How does the use of chemical information influence the population dynamics of and the interactions between species at consecutive trophic levels in a food chain? At a more detailed level: Why does a host species use an aggregation pheromone when aggregating can result in increased competition and the communication used to aggregate can be spied upon by a natural enemy?

A trait can evolve when, for an individual carrying that trait, the benefits are higher than the costs. Costs and benefits are often expressed in terms of the Darwinian fitness of an individual, i.e. its lifetime reproductive success - how many offspring it can produce over its lifetime in combination with the quality of that offspring. For a trait to be selected for individuals with this trait should have a higher lifetime reproductive success than individuals without this trait.

In this study, I do not intend to investigate how the use of the aggregation pheromone cis-vaccenyl acetate has evolved in *D. melanogaster*. Instead, I look at the present-day situation where both fruit flies and one of its natural enemy species can use chemical information. By using simulations, I study the effect of the use of chemical information on the population dynamics of the host. I start by investigating the effect of chemical information on the population dynamics of *D. melanogaster* in the absence of a natural enemy. The use of aggregation pheromone can possibly play an important role during colonization. Therefore, I do not only study the effect on population dynamics and the larval survival when the fruit fly population is already present in the breeding area at the beginning of the season. I also address the effect of chemical information when a fruit fly population is situated outside the breeding area at the beginning of the season, and has to colonize the breeding area before reproduction can start. Next, I study the effect of the use of chemical information on the population dynamics and the larval survival of the fruit fly in the presence of the parasitoid *L. heterotoma* that can spy on *D. melanogaster*'s intraspecific communication, and compare it with a situation where fruit flies and/or the parasitoid cannot use chemical information. In this study, I address the ecological costs of chemical communication that arise from adult crowding and an eavesdropping parasitoid at the population level. As a measure for the costs and benefits of the use of chemical information, I consider population growth, population size, and local larval survival. Finally, I investigate how fruit flies may track an odour plume and discriminate between odour sources that differ in suitability for reproduction. I specifically look at fruit fly arrival and spatial distribution of the arriving fruit flies.

Part I: Chemical communication - Fruit fly population response to chemical information

In **Chapter 2** I introduce a spatio-temporal model that describes the movement of a fruit fly population, by computing the spatially varying density of fruit flies in a given area at consecutive points in time. It incorporates odour distribution and calculates the fruit fly responses thereupon, by computing fruit fly population dynamics, both within a population (i.e. spatial population distribution and settlement on the odour sources) and between generations (i.e. local larval survival). For these long term simulations, I assume that odours are distributed randomly in the environment and thus are distributed evenly in each direction. This model is used to investigate the costs and benefits of the use of infochemicals when no natural enemy is present, by comparing both the population size and the larval mortality due to the Allee effect or competition between the three different responses to chemical information of the fruit flies: (1) that cannot respond to chemical information and thus can only disperse randomly, (2) that can respond to only food odours or (3) that can respond to both food odours and its aggregation pheromone. In **Chapter 3** I discuss the chosen values for the model parameters of the population model of **Chapter 2** and perform a sensitivity analysis.

In **Chapter 2**, my research hypothesis is that the use of chemical information mainly has a positive effect on the fruit fly population when the population is small, because then the Allee effect plays an important role. These small population numbers are typically found in the build-up phase of a population. In the Dutch climate, fruit flies hibernate in man-made structures, and at the end of the winter, only a fraction of the original population has survived. Before they can reproduce they must re-colonize their natural habitat in spring. In **Chapter 4**, I explore the effect of chemical information usage when the fruit fly population colonizes an orchard from outside the domain. In this situation, the chance of finding a suitable resource by random movement is quite low. I hypothesize that in this situation guidance of the fruit flies by chemical information plays a more profound role in locating the resources and conspecifics than in the situation in **Chapter 2**, where the initial fruit fly population was situated in the centre of the domain. To study the impact of the Allee effect on population dynamics, I also address the situation without an Allee effect.

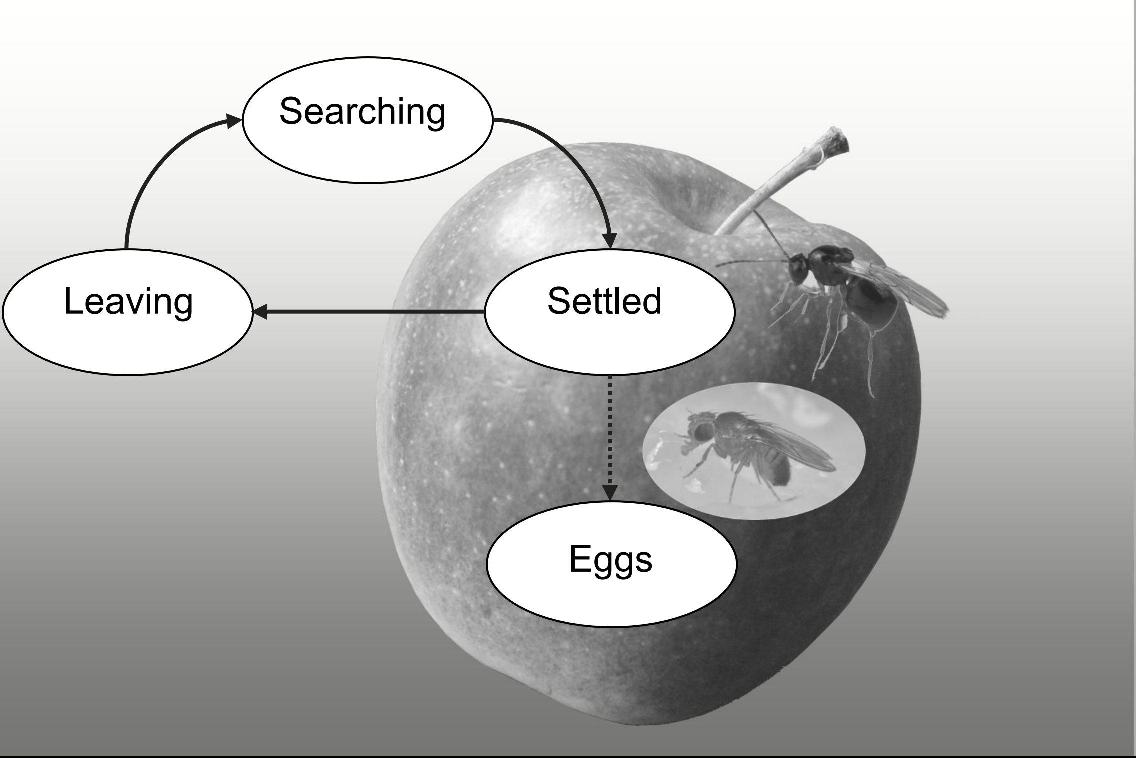
Part II: Chemical espionage – Odour-mediated parasitoid-host interactions

In **Chapter 5** I examine how chemical information affects the interaction between hosts and parasitoids. For this purpose, I extend the spatio-temporal model developed in **Chapter 2** that modelled infochemical distribution and fruit fly population dynamics with the population dynamics of the parasitoid and the interaction between the parasitoid and the host. The larval parasitoid *L. heterotoma* spies on the aggregation pheromone of the adult fruit flies to find its hosts, i.e. the larvae of the fruit fly. In this chapter, I study whether the use of chemical information is still beneficial for the fruit flies when a natural enemy can spy on its intraspecific communication. I compare fruit fly larval survival and population size of randomly dispersing fruit flies with larval survival and population size of fruit flies using chemical communication, in the presence of a parasitoid that either disperses randomly, or can use chemical information. To test the hypothesis that fruit flies experience an additional cost associated with the use of aggregation pheromone as a result of an increased mortality due to parasitism, I compare the fruit fly population dynamics in the case that the parasitoid can only use odours emitted by the host habitat, i.e. food odours, with the case that the parasitoid can use both odours emitted by the host habitat and the aggregation pheromone of the fruit flies. As a reference I also address fruit fly population dynamics when no parasitoids are present. A possible advantage of aggregation is that an individual can 'hide' in the group and has a lower chance of being attacked by a natural enemy. To test whether fruit fly larvae experience a diluted risk of attack at high larval densities, I investigate how local (e.g. per resource) mortality due to parasitism relates to larval density.

Part III: Chemical discrimination – How individual fruit flies track odour plumes

Chemical information becomes available to flying insects when molecules are distributed into the environment by wind and turbulent diffusion. In **Chapter 6** I introduce individual-based models for odour-oriented flight patterns of individual fruit flies. In these models, I let fruit flies respond to a filamentous plume model (Farrell et al, 2002), that takes many features of a real odour plume into account. Modelling of odour plume tracking has focused only on behavioural rules that animals use to track one odour plume (Sabelis and Schippers, 1984; Weisburg et al., 2002). In reality, animals often are in a situation where several odour sources are present that differ in attractiveness. In **Chapter 6**, we investigated which behavioural decisions enhance the ability to find - and distinguish between – different odour sources. Starting point for our individual-based model for fruit fly movement was an individual-based model for sex-pheromone oriented flight of male moths (Yamanaka et al., 2003), that we parameterized for *D. melanogaster* (Budick and Dickinson, 2006). To explore which individual-based model for odour-oriented flight could describe the spatial distribution and arrival on the patches of *D. melanogaster* best, they are benchmarked in a simulation set-up where flies could use infochemicals for choosing between resources of varying suitability for reproduction. The model outcomes were compared with experimental findings of Wertheim et al. (2002a).

A summarising discussion of the results is presented in **Chapter 7**. Here, I also discuss future directions in understanding the effect of chemical information on population dynamics of species in a food web.



Pictures Hans Smid (Bugsinthepicture.com)

The effect of chemical information on the spatial distribution of fruit flies

I Model results

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Abstract

Animal aggregation is a general phenomenon in ecological systems. Aggregations are generally considered as an evolutionary advantageous state in which members derive the benefits of protection and mate choice, balanced by the costs of limiting resources and competition. In insects, chemical information conveyance plays an important role in finding conspecifics and forming aggregations. In this study, we describe a spatio-temporal simulation model designed to explore and quantify the effects of these infochemicals, i.e. food odours and an aggregation pheromone, on the spatial distribution of a fruit fly (*Drosophila melanogaster*) population, where the lower and upper limit of local population size are controlled by an Allee effect and competition. We found that, during the spatial expansion and strong growth of the population, the use of infochemicals had a positive effect on population size. The positive effects of reduced mortality at low population numbers outweighed the negative effects of increased mortality due to competition. At low resource densities attraction towards infochemicals also had a positive effect on population size during re-colonization of an area after a local population crash, by decreasing the mortality due to the Allee effect. However, when the whole area was colonized and the population was large, the negative effects of competition on population size were larger than the positive effects of the reduction in mortality due to the Allee effect. The use of infochemicals thus has mainly positive effects on population size and population persistence when the population is small and during the colonization of an area.

Keywords Chemotaxis · Aggregation · Integro-difference equations · Spatial population dynamics · Allee effect

2.1. Introduction

Many studies indicate that animal aggregation is a general phenomenon in ecological systems (Parrish and Edelstein-Keshet, 1999; Wertheim et al., 2005). Forming an aggregation can be beneficial to individuals as a result of overcoming difficulties that are associated with low population densities, such as finding a mate (Parrish and Edelstein-Keshet, 1999; Wertheim et al., 2005) or overcoming resource resistance (Wertheim et al., 2002, 2005). In addition, protection from predators is considered to give important selective advantage to group membership of individuals (Krebs and Davies, 1997; Wertheim et al., 2005). However, aggregations can also involve costs. At large group sizes, individuals compete for resources or suffer density-dependent predation and disease (Parrish and Edelstein-Keshet, 1999; Wertheim et al., 2005).

Animal aggregations can arise when individuals respond behaviourally to the presence of conspecifics and actively search for each other. This is possible only if individuals release information on their whereabouts, either deliberately or involuntarily as a result of their activities. Conspecifics that receive this information can exploit it to adjust their behaviour. The cues that are concerned in such information conveyance can be visual, auditory, tactile, or chemical. In insects, as in many other animals, chemical information conveyance is of profound importance (Bell and Cardé, 1984, 1995; Cardé and Minks, 1997; Schoonhoven et al., 2005). The chemicals involved in the chemical information conveyance are termed info- or semiochemicals, and can influence both intra- and interspecific interactions (Dicke and Sabelis, 1988).

The chemicals that specifically induce group formation are termed aggregation pheromones. The chemical composition of aggregation pheromones and attraction of insects to them has been studied in great detail (Bartelt et al., 1985; Schaner et al., 1987; see also Wertheim et al., 2005). In addition, the searching behaviour of insects in odour plumes has been studied in the laboratory and in the field (Cardé, 1984; Murlis et al., 1992; Bell et al., 1995) and mathematical models for odour plumes and plume tracing models for individual insects or autonomous robots have been developed (Sutton, 1953; Yamanaka et al., 2003; Farrell et al., 2002). These studies focus on short term behavioural responses of individual insects. However, no studies have been reported on the long term effects of infochemical use and its effect on spatial population dynamics.

In this paper, we study the implications of infochemical use on population dynamics of a single species in a spatial context, by adopting a spatio-temporal approach that incorporates odour dispersal and organismal responses. We use *Drosophila melanogaster* as a model organism. Drosophilid fruit flies breed in various ephemeral substrates like decaying materials, fermenting fruits, fungi, and sap streams. Therefore, the place where an adult emerges from its pupa often contains no food anymore. Thus, the life of adult fruit flies generally starts with the task of locating a suitable substrate where they can eat, mate, and where females can oviposit. Chemical attraction toward fermentation products produced by microorganisms that live on food sources and aggregation pheromones emitted by recently mated adult female fruit flies play a directive role in the selection of these substrates (Hutner et al., 1937; West, 1961; Bartelt et al., 1985; Wertheim, 2001). Moreover, the combination of aggregation pheromone with food odours is more attractive than food odours alone (Bartelt et al., 1985).

The use of aggregation pheromones can only evolve when individuals benefit from clustering. This situation can occur when an Allee effect plays a role, which is the phenomenon that for smaller populations the per capita growth rate is lower than for intermediate population sizes due to lower reproduction or higher mortality (Allee, 1931). In *D. melanogaster,* its aggregation pheromone induces aggregated oviposition. The presence of adults prior to larval development increases the amount of food that is present for the larvae; adults (especially females) vector a diversity of yeasts and inoculate the resource with these yeasts during their presence (Morais et al., 1995). Furthermore, Wertheim et al. (2002) showed that increased adult densities prior to larval development reduced fungal growth. It is known that strong fungal growth can cause a high mortality in fruit fly larvae (Rohlfs et al., 2005; Rohlfs, 2006). Adult aggregation thus has a positive effect on larval survival by altering the suitability of the resource. Forming aggregations is not only beneficial. Rohlfs and Hoffmeister (2003) show that the survival from egg to adulthood for *Drosophila subobscura* is hump shaped, with low survival not only at low population numbers, but also at high population numbers. Thus, there also is a risk in aggregation. At high local population densities, larval survival decreases due to competition (Wertheim et al., 2002; Hoffmeister and Rohlfs, 2001).

Etienne et al. (2000, 2002) studied how the Allee effect, scramble competition, and nondirected dispersal affected population dynamics of *D. melanogaster*. They found that local instability in population numbers could be balanced by dispersal. In reality, the dispersal of fruit flies is not random, but directed by the response to infochemicals. We investigate to what extent the presence of infochemicals, specifically food odours and aggregation pheromone, affect the spatial distribution of a fruit fly population and whether infochemical-directed dispersal can balance local population instability. Furthermore, we investigate the positive and negative effects of the use of infochemicals on population numbers, by addressing larval mortality due to Allee effect and competition and the net effect on population numbers. We expect the use of infochemicals to promote population persistence in a heterogeneous unpredictable environment in space and time, where colonization and recolonization after local extinction are important processes.

2.2. Description of the model

Odour distribution and the insects' responses are by definition spatial processes. Therefore, a spatio-temporal model is the most appropriate approach to gain insight into the effect of infochemicals on population dynamics.

2.2.1 Dispersal of fruit flies and population dynamics

The reproductive life of female fruit flies generally starts with searching for a suitable resource. When they find a resource they settle to feed, mate and oviposit. Thereafter, they leave the resource to search for another suitable resource. To model these different activities, we divided the adult population density H into three activity states: a searching state C (with fly density H_C), in which individuals fly in the air and use infochemicals that are present in the air to find a suitable resource, the moment they find a resource and land they come into a settled state S (with fly density H_S), in which individuals spend time on a resource, and a leaving state L (with fly density H_L), in which individuals actively fly away from the resource. In our model, the total adult population remains constant within a generation; there is no adult immigration, emigration, or mortality. Furthermore, we only modelled the adult females. In *Drosophila melanogaster,* adult males produce the aggregation pheromone (cis-vaccenyl acetate) and transfer it to females during mating (Bartelt et al., 1985). Recently mated females then emit the aggregation pheromone. The amount of aggregation pheromone emitted by males is very small compared to the amount that the females emit. In addition, Bartelt et al. (1985) showed that both sexes respond similarly to the aggregation pheromone. We, therefore, assumed that the distribution of females gives a good representation of the distribution of the whole fruit fly population and that the adult female population dynamics could be modelled satisfactorily without considering the adult males.

2.2.1.1 Dispersal of fruit flies

The dispersal of searching fruit flies (*C*) is random in the absence of infochemicals. In the presence of infochemicals, however, the movement of searching fruit flies is usually directed toward the source of the odour. We assume that *D. melanogaster* only uses a concentration gradient to find the odour source and that dispersal can be modelled with a two-dimensional chemotaxis model for the redistribution of flies.

Powell et al. (1998) gave a general format for chemotactic movement in biology. We used this format to model the population responses toward a concentration gradient of the food odour (*F*) and aggregation pheromone (*A*)

$$\frac{\partial}{\partial t} H_C = D_H \nabla^2 H_C - \nabla \cdot \left[v\, H_C\, \nabla f(F, A) \right] \tag{1}$$

where H_C is the density of the searching *Drosophila* population, v is the attraction constant of the infochemicals, f is the effective sensory index of *D. melanogaster* with respect to F and A (see below), and D_H is the dispersal constant of the searching population.

Sensory index

Bartelt et al. (1985) showed two important features concerning the responses of *D. melanogaster* toward food odours (blend of fermentation products and yeast odour) and its aggregation pheromone: (1) the aggregation pheromone is only attractive when food odours are present; (2) *D. melanogaster* is about four times more attracted to the combination of food odours and its aggregation pheromone than to food odours alone. A description of the response of *D. melanogaster* to infochemicals that is consistent with these findings is:

$$f(F, A) = \frac{F}{F_0 + F} + \eta \frac{FA}{F_0 A_0 + FA} \tag{2}$$

where F and A are the food odours and aggregation pheromone respectively; F_0 and A_0 are the corresponding half saturation values, and η represents the attraction ratio of food odour in combination with aggregation pheromones (F+A) relative to the attraction to food odour alone (F).

Leaving the resource

While the movement of searching fruit flies is directed by infochemicals, the movement away from the resource by the leaving fruit fly population (*L*) in the model is not considered to be affected by the presence of food odours and aggregation pheromone. The movement of the moving population is described by ring-random dispersal, where fruit flies first actively fly away from the resource and then distribute randomly (see Eq. 9). We chose this type of dispersal to achieve that a large part of the moving population actually does leave the resource. Without first flying away from the resource, the largest part of the fruit flies would remain on the resource.

2.2.1.2 Population dynamics

Within-generation dynamics

The total adult population is held constant within a generation, and there is no migration over the boundaries of the spatial domain (reflecting boundary conditions). However, the distribution of individuals over the three activity states does change over time (Fig. 1). When a searching individual finds a resource (*R*) it settles on the resource with settlement probability α_1 (min^{-1}). Settled individuals leave the resource at a constant rate, the patch leaving probability, α_2 (min^{-1}). A moving individual that has left the resource starts searching again with a probability α_3 (min^{-1}). The distribution of the resources (i.e. yeast-infected apples) and local within-generation population dynamics in each point in space (*x*, *y*) (see section 2.4) are described by the following equations

$$R(x,y)=\begin{cases}0 & \text{if no apple is present at position } (x,y) \text{ at time } t\\ 1 & \text{if an apple is present at position } (x,y) \text{ at time } t\end{cases} \tag{3a}$$

$$\frac{\partial}{\partial t}H_C=\alpha_3 H_L-\alpha_1 R H_C \tag{3b}$$

$$\frac{\partial}{\partial t}H_S=\alpha_1 R H_C-\alpha_2 H_S \tag{3c}$$

$$\frac{\partial}{\partial t}H_L=\alpha_2 H_S-\alpha_3 H_L \tag{3d}$$

From here on we refer to yeast-infected apples simply as apples. Values for the parameters used are given in Table 1. For more details on how these values are arrived at, we refer to the companion paper (de Gee et al., 2008; **Chapter 3**).

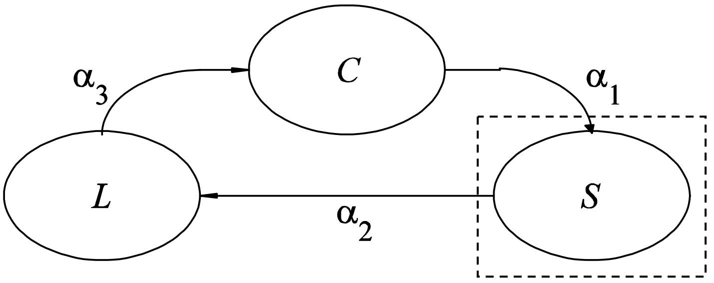

Figure 1 Schematic representation of the population dynamics. The total population is divided into three activity states, *C* the searching part of the population, *S* the settled part of the population, *L* the leaving part of the population, with α_1, α_2 and α_3 the transition rates. The dashed block represents a resource.

Between-generation dynamics: reproduction

Adult females that have settled on a resource (*S*) deposit ξ eggs per minute on average. The cumulative number of eggs (*N)* on each resource item after 3 days (in generation *n*) determines whether larvae develop successfully into adults (Eq. 4). The percentage of the larvae on one substrate that survives depends on the number of larvae present, survival is best for intermediate numbers of larvae. When there are only a small number of larvae on an apple, a fraction dies due to the Allee effect, while mortality due to competition plays a role when there are many larvae present. Of the surviving larvae a fraction φ is female and these constitute the next female adult generation.

$$N(x,y,n)=\int_0^3 \xi\, H_S(x,y,n)\,dt \tag{4}$$

The number of larvae becoming adult females in the next generation $H(x,y,n+1)$ depends on the survival probabilities for the Allee effect ($s_A(N)$) and for competition ($s_C(N)$) in the following way

$$H(x,y,n+1)=\varphi\cdot N(x,y,n)\cdot s_A(N)\cdot s_C(N) \tag{5}$$

with

$$s_A(N)=\frac{1}{1+e^{-c_A(N-N_A)}} \tag{6a}$$

$$s_C(N)=1-\frac{1}{1+e^{-c_C(N-N_C)}} \tag{6b}$$

where $H(x, y, n+1)$ denotes the newly emerged adult females that start searching immediately (C). The graphs of these functions are sigmoid curves with values between 0 and 1. The functions $s_A(N)$ and $s_C(N)$ are increasing and decreasing respectively, the parameters c_A and c_C affect the slope of this increase or decrease and N_A and N_C are the number of larvae at which the survival rate is 50 %.

2.2.2 Infochemical distribution

D. melanogaster responds to food odours (F) and its aggregation pheromone (A). In this model, we assume that there is no wind and that these odours thus diffuse randomly, with an equal probability to go in all directions. Odour diffusion is a much faster process than the dispersal of adult fruit flies. In addition, odour diffusion is a 3-dimensional process, while we model in two dimensions. We therefore introduced a loss term to represent odour matter that gets out of reach of the searching population by diffusion in the vertical direction (see also de Gee et al., 2008; **Chapter 3**). Aggregation pheromone is not excreted in a gaseous form, but as a fluid accompanying the eggs. We, therefore, divide the aggregation pheromones in two phases: a liquid form on the resource that slowly evaporates (A_R), and a gaseous form (A) that is detectable for the searching fruit flies in the air. The distribution of food odours and aggregation pheromone can thus be modelled by

$$\frac{\partial}{\partial t}F = D_I\nabla^2 F-\mu F+\theta_F R \tag{7a}$$

$$\frac{\partial}{\partial t}A = D_I\nabla^2 A-\mu A+\omega A_R \tag{7b}$$

$$\frac{\partial}{\partial t}A_R = \theta_A H_S-\omega A_R \tag{7c}$$

respectively, where D_I is the diffusion constant of the infochemicals, μ is the average loss rate of the infochemicals in the z-direction, the value of this loss rate is dependent on the average time used. For more details on odour loss we refer to de Gee et al., 2008 (**Chapter 3**). As dispersal and loss are mainly driven by atmospheric turbulence, these parameters have the same value for both food odours and aggregation pheromone. Furthermore, θ_F and θ_A are the production rates of the food odour by the resource (R) and the aggregation pheromone by the settled population (H_S) respectively and ω is the odour release rate by evaporation.

2.2.3 Integro-difference equation (IDE) approach

The model derived contains spatial dispersion of fruit flies and odours. Therefore, the system of ordinary differential equations that result after spatial discretization is stiff. This means that it contains a range of different timescales; while we are interested in the process at the slowest timescale, the fastest time scale may control the numerical stability of explicit methods for solving this system of ordinary differential equations. In our case, this situation is aggravated by the fact that the odour distribution is a much faster process than the dispersal of fruit flies. Therefore, simple explicit integration methods are unsuitable because of a small step size, while on the other hand, the nonlinearity of the model impedes the use of implicit integration methods. For this reason we chose the integro-difference approach (as in Neubert et al., 1995, Powell et al., 1998 and Etienne et al., 2002), which treats the dispersion as a separate process that can be solved analytically. This approach is effective because it allows us to take large time steps in accordance to the slow process, without running into any stability problems. In this approach dispersal and population dynamics (e.g. reproduction) are treated as two distinct phases; we model odour and fruit fly dispersal separate from adult population dynamics.
The dispersal of the population is calculated by taking the convolution product of the population density and the dispersal probability function. We take dispersal to be described by one of the following two-dimensional probability density functions or dispersal kernels (eqs. 8 and 9). Random dispersal, used for modelling the dispersal of the searching population and for odour diffusion is described by

$$K_{RD}(x,y,\Delta t)=\frac{1}{4\pi D\Delta t}\,e^{-\frac{x^2+y^2}{4D\,\Delta t}} \tag{8}$$

where Δt is the time step taken and D is the dispersal constant of the fruit flies (D_H) or the diffusion constant of the infochemicals (D_I). Ring random dispersal, used to model the moving population, is described by

$$K_{RR}(x,y,\Delta t)=\frac{1}{4\pi D_H\,\Delta t}\,e^{-\frac{(\sqrt{x^2+y^2}\,-\,\rho\Delta t)^2}{4D_H\Delta t}} \tag{9}$$

where ρ is the velocity of the displacement away from the resource.

The random dispersal kernel above, models the diffusion of the odour that is already present in the system. During each time step, odour is produced by the resources and released into the air. The dispersal of the produced odour is calculated by taking the convolution product of the odour produced per minute and a dispersal probability function for a continuously producing source. The distribution of the produced odour is described by Eq. 10.

$$K_S(x,y,\Delta t)=\int_0^{\Delta t}\frac{1}{4\pi D_I t}\,e^{-\frac{x^2+y^2}{4D_I t}}\,dt=\frac{1}{4\pi D_I}\,Ei\left(\frac{x^2+y^2}{4D_I\Delta t}\right) \tag{10}$$

where *Ei* is the exponential integral.

The infochemicals direct the movement of the searching population toward the odour source. The spatial distribution of searching fruit flies, resulting from Eq. 1, can, according to Powell et al. (1998), be approximated in discrete time by

$$H_C(x,y,t+\Delta t) = \psi e^{\kappa f(F,A)} K_{RD}(x,y,\Delta t) * \left\{ e^{-\kappa f(F,A)} H_C(x,y,t) \right\} \quad (11)$$

where K_{RD} is the random dispersal kernel for the population of fruit flies and ψ a normalization constant. The '$*$' denotes the convolution operator over all spatial coordinates, i.e.:

$$(p*q)(x,y) = \iint p(x-x', y-y') q(x', y') dx' dy' \quad (12)$$

In equation 11, chemotaxis is modelled as a diffusion process. Diffusion is the movement of materials from an area with a high density to an area with a low density until equilibrium is reached. We can model movement toward the attractive source by artificially reducing the population density, with a stronger reduction for a more attractive spot. As diffusion occurs from high densities to low densities, the reduced population diffuses toward the attractive source, because the population density is—artificially—low at and around the source.

Equation (11) is best interpreted when it is read from the right to the left. It describes how the population at time t is first multiplied by a factor that contains the sensory index of the species and the attraction ratio κ (= v/D_H). This multiplication amounts to rescaling the population density. It strongly decreases the population density at points with a high odour concentration (combination of food odour and aggregation pheromone), while the density remains approximately the same where odour concentration is low. The dispersal is now directed toward the points with a low—rescaled—population density. After dispersal, the rescaled population is scaled back with the inverse of the above mentioned factor. This results in a strong increase of the population density in points with a high odour concentration. In this way, dispersal with a bias directed toward the infochemicals is modelled. However, this dispersal is not completely mass-conservative when using numerical approximations. Therefore, the dispersal step is finalized by normalization. To this end, we multiply the resulting density after chemotactically driven diffusion by such a number ψ that the total number of searching fruit flies is preserved.

Attractiveness to infochemicals

The dimensionless ratio $\kappa = v/D_H$ is a measure for the relative strength of the chemical attraction (v) as compared to the random dispersal (D_H). If there is no chemical attraction, then the movement is at random and $\kappa = 0$. On the other hand, a strong influence of the chemical attraction in comparison to the random dispersion corresponds to high values of κ. In that case, the movement is directed toward the odour source.

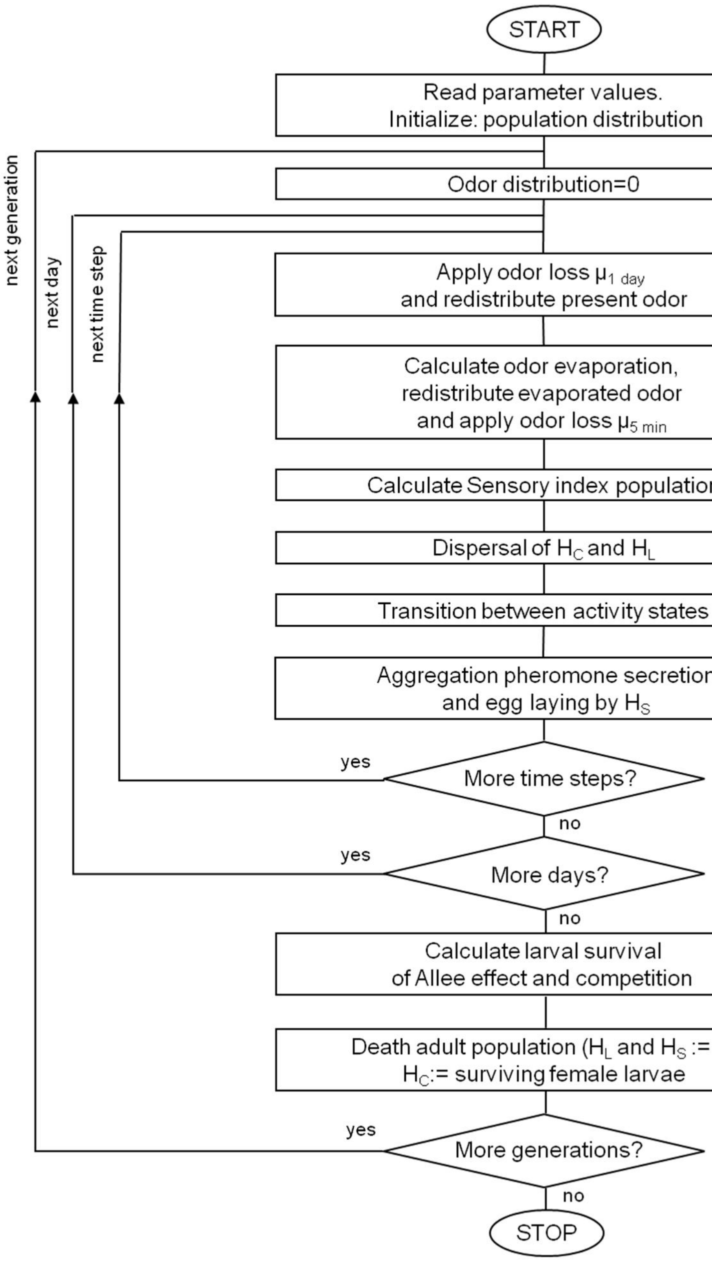

Figure 2 Flow chart of the processes in the model. In our model the time step, *Δt*, is 5 min. We simulated 1 generation in the short term simulation and 10 generations in the long term simulation. Each generation consisted of 3 days.

2.2.4 Simulation

We considered a square spatial domain with reflecting boundary conditions for the population of fruit flies, and absorbing boundaries for the infochemicals. The reflecting boundary conditions for the flies represent a closed system (they cannot escape). On the other hand, the infochemicals can freely pass through the boundaries, never to come back: this is modelled by the absorbing boundary condition. We ran simulations for one generation, consisting of 3 dispersal days (short term population dynamics) and 10 generations of 3 dispersal days (long term population dynamics). Because evaporation is temperature dependent, odour evaporation during the night is much smaller than during the day. Also, the activity of yeasts, the main producers of the attractive fermenting fruit smell, is temperature dependent. We, therefore, assume that during the night no odour is produced. Furthermore, we assume that fruit flies do not reproduce or disperse during the night. Therefore, we modelled 12 hours per day. We discretised each dispersal day in steps of 5 minutes of dispersal by adult females followed by population dynamics (i.e. by settlement on resource, reproduction, patch leaving or start of searching behaviour) (Fig. 2).

2.2.4.1 Short term (one generation) simulation

To study the basic distribution patterns of fruit flies in a two-dimensional environment where infochemicals are present or absent, we ran three simulations, one “control” simulation where no odours were present, one simulation where only food odours were present ‘F’, and a simulation where both food odours and aggregation pheromone were present ‘F+A’. We simulated the dispersal of fruit flies on a spatial domain of 30 m×30 m. It is divided into 256×256 cells with a diameter of 0.117 m. The factor 256 is not essential for the design of the experiments, nor does it influence the results essentially; however, it enhances the efficiency of the numerical computations, because powers of 2 allow use of the fast Fourier transform for the convolutions.

Initial distribution of resources

We are interested in spatial differences due to aggregation. We therefore divided the domain in four quadrants. Each quadrant contained 9 resource patches of 1m^2 clustered in one block (of 5 m × 5 m), with an interpatch distance of 1 m (Fig. 3a). The blocks were situated 6.5 m from the boundaries of the domain. The distance between two adjacent blocks was 7 m. The initial resource density was 5 apples m^{-2}, evenly distributed over the block (like apple-sauce).

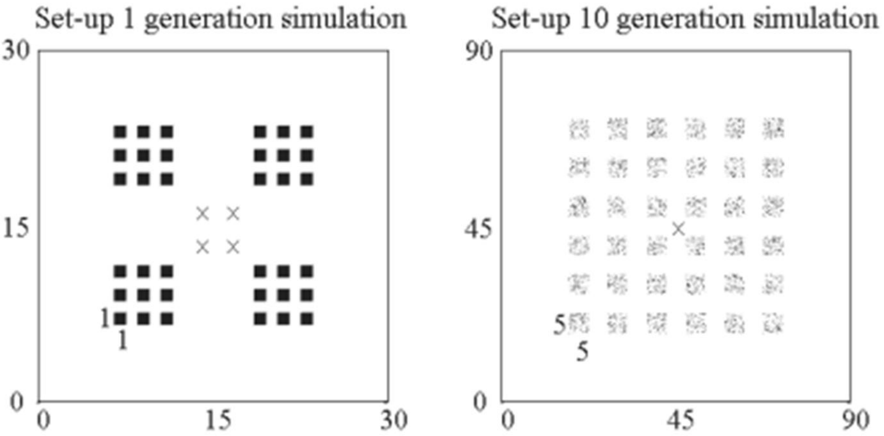

Figure 3 The set-up of the domain with spatial dimensions of the (a) short term simulation, size 30m×30m, with 4 blocks of 9 clustered resources with resource density of 5 apples m^{-2}, and the (b) long term simulation, size 90m×90m, with 36 blocks containing randomly distributed apples with resource density of 5 apples m^{-2}.The release point of the initial population is denoted with (x).

Initial adult distribution

To study whether aggregation occurs at resources with a higher initial density, we unevenly divided 800 adults (H_0) over the four quadrants. We situated 500 females in the lower left quadrant and 100 females in each of the other three quadrants. The fruit flies were released near the centre of the domain. The release points were situated 2.5 m from the nearest resource. The distance between the release points in the centre was 3.5 m.

Larval survival

At the end of the generation the larval survival is calculated. We assessed the number of larvae that successfully developed into an adult female. In addition, to determine the costs and benefits of the use of infochemicals we also assessed the number of larvae that did not survive due to the Allee effect or due to competition, and calculated mortality rates for both effects separately.

Statistics

To calculate the degree of aggregation of the population we use k a measure of the amount of clumping, given by

$$k = \frac{\mu^2}{\sigma^2 - \mu} \qquad (13)$$

where μ is the mean and σ^2 the variance of the negative binomial distribution (Southwood and Henderson, 2000). The smaller the value of k, the greater the extent of aggregation, whereas for $k \to \infty$ (i.e. in practice $k > 8$) the distribution approaches a Poisson distribution, i.e. is virtually random. The value of k is influenced by the size of the sampling unit. In our model we use same-sized units. Thus, we are able to use this measure to compare the degree of aggregation for the different treatments of availability of infochemicals.

To test the effects of infochemical use on settlement and on larval survival we used the G-independence test on the number of settled and moving fruit flies for each treatment or on the number of larvae that survived or died for each treatment (Sokal and Rohlf, 1981). The short term simulation is also used for a sensitivity analysis. For more details on the sensitivity analysis, we refer to our companion paper (de Gee et al., 2008; **Chapter 3**).

2.2.4.2 Long term (ten generations) simulation

To study the long term population dynamics, we modelled a fruit fly population in an unpredictable heterogeneous environment. *D. melanogaster* cannot survive the winter in the natural climate of the Netherlands. Therefore, we simulated only one breeding season, consisting of 10 discrete generations. We model discrete nonoverlapping generations of 3 days each. These days consist of 12 dispersal hours, divided in time steps of 5 minutes (Fig. 2). The larval development was lumped, and computed at the end of the generation. For the long term simulation we considered a domain of 90 m × 90 m, divided into 512×512 square cells, each with a diameter of 0.176 m. We ran three simulations, one 'control' simulation where no odours were present, one simulation where only food odours were present 'F', and a simulation where both food odours and aggregation pheromone were present 'F+A'.

Initial adult and resource distribution

We introduced 2,000 fruit flies (H_0) in one single cell in the centre of the domain.

This domain contains 36 resource blocks of 5 m×5 m (Fig. 3b). The resource blocks were situated 17.5 m from the boundaries of the domain. The distance between two adjacent blocks was 5 m. The initial resource density was 1 apple m^{-2}. To study at which spatial scale effects take place we looked at the population dynamics at a large spatial scale, i.e., the four quadrants of the domain (each containing 9 resource blocks), at an intermediate spatial scale, i.e. the resource blocks and 2.5 meter around the blocks and at a small spatial scale, i.e. individual apples. For the simulation at the largest spatial scale we used two additional resource densities, 5 and 10 apples m^{-2} to study whether the spatial dynamics of the fruit fly population depends on resource availability.

To mimic the natural situation, the apples were placed randomly each generation, with each grid cell in the block containing either one apple or no apple (Eq. 3a). Outside the resource blocks the cells were empty. The total amount of apples per quadrant of the domain was fixed (for example, when the initial resource density is 1 apple m^{-2}, a quadrant contains 9 (blocks) × 25 (m^2) × 1 (apple m^{-2}) = 225 apples) but as they were placed randomly over the resource blocks, there were differences in the amount of apples per resource block.

We ran the simulations at the largest spatial scale three times, with a different starting point of the random number generator, to verify the consistency of the results.

Statistics

We used linear mixed models to test the effect of the use of infochemicals on the mortality due to the Allee effect (%), mortality due to competition (%), and larval survival (%) in the first five generations (during the population expansion). This method is especially suitable for data, where the measurements are correlated in time. In the model, we took “generation” as repeated measurement, and “treatment”, “generation”, and “treatment × generation” as fixed effects. We tested the model for four different covariance structures, compound symmetry (CS), first-order autoregressive (AR(1)), heterogeneous first-order autoregressive (ARH(1)), and an unstructured covariance matrix (UN). The unstructured covariance matrix was the best model for the data (it had the lowest AIC). For these statistics we used SAS 9.1.

2.2.5 Parameter values

We used the parameter values as given in Table 1. For more details on how these values are arrived at, we refer to the companion paper (de Gee et al., 2008; **Chapter 3**).

Table 1 The model parameters involved in the short time dynamics and their values.

Name	Description	Value	Units
D_H	Dispersion coefficient of at random moving fruit flies	0.058	$\mathrm{m}^2\ \mathrm{min}^{-1}$
α_1	Settlement rate of searching fruit flies	0.25	min^{-1}
α_2	Rate of settled fruit flies leaving the resource	0.002	min^{-1}
α_3	Rate of moving fruit flies that start searching for resources	0.5	min^{-1}
ρ	Velocity of movement away from the resource	1	$\mathrm{m\ min}^{-1}$
F_0	Saturation parameter for food odours	10	$\mathrm{ng\ m}^{-2}$
A_0	Saturation parameter for aggregation pheromones	0.04	$\mathrm{ng\ m}^{-2}$
D_I	Dispersion rate of infochemicals	1	$\mathrm{m}^2\ \mathrm{min}^{-1}$
$\mu(720)$	Loss rate of infochemicals	0.025	min^{-1}
$\mu(5)$	Loss rate of recently produced infochemicals	0.171	min^{-1}
θ_F	Food odour production by the resource	2	$\mathrm{ng\ apple}^{-1}\ \mathrm{min}^{-1}$
θ_A	Aggregation pheromone production by settled fruit flies	0.83	$\mathrm{ng\ fly}^{-1}\ \mathrm{min}^{-1}$
ω	Evaporation rate of liquid aggregation pheromone	4.10^{-4}	min^{-1}
v	Attraction towards infochemicals	$5D_P$	-
κ	Relative strength of movement towards infochemicals compared to random dispersal	5	-
η	Attraction ratio of food odour together with aggregation pheromones relative to the attraction to food odour alone	2.51	-
ξ	Fecundity of the settled population	0.0083	min^{-1}
φ	Sex ratio of the larvae (fraction of females)	0.5	-
N_A	Number of larvae per apple at which 50 % survives the Allee effect	25	-
N_C	Number of larvae per apple at which 50% survives competition	250	-
c_A	Slope sigmoid survival curve modelling the Allee effect	0.088	-
c_C	Slope sigmoid survival curve modelling the competition	0.044	-

For dimensionless parameters the '-' sign is used.

2.3. Results

2.3.1 Short term (one generation) simulation

In our model, the infochemicals affect, as expected, the spatial distribution of the fruit flies. When both food odours and aggregation pheromone are present (F+A), the distribution of the total population ($H_C + H_S + H_L$) over the quadrants after one generation is significantly different from the control situation where no chemical information is present ($\chi^2_{(3)}$=150.64, $p < 0.0005$) or where only food odours are present (F, $\chi^2_{(3)}$=115.59, $p < 0.005$). This can also be seen if we look at the measure for clustering: k changes from 47.73 (control) to 23.52 (F) to 2.16 (F+A) with increasing availability of chemical information. Increasing the chemical information present thus causes the population to distribute less randomly. This indicates that aggregation occurs when both food odours and aggregation pheromones are present (F+A) (Fig 4).

We have also compared the distribution of settled fruit flies (H_S) over the four quadrants (Fig. 4, lower part bars). The distributions of the settled populations for both F+A and F turns out to be significantly different from the control situation ($\chi^2_{(7)} = 216.97$ (F+A), $\chi^2_{(7)} = 51.93$ (F), both $p < 0.0005$). For the settled fruit fly population the clumping parameter (k) changes from 43.31 (control) to 21.50 (F) to 1.96 (F+A). The distribution of settled fruit flies when both food odours and aggregation pheromone are present differs also significantly from the distribution with only food odours ($\chi^2_{(7)} = 116.97$, $p < 0.0005$). The different distribution, combined with the lower value for the clumping measure, indicates that the availability of aggregation pheromone indeed mediates aggregation.

The percentage of the total adult population that settled on the resources after one generation is higher when chemical information is present. For the quadrant with the highest initial density, the settlement increases from 73.8% in the control situation without infochemicals, to 85.0% (F, G = 4.84, p < 0.05) and 86.3% (F+A, G = 7.63, p<0.01) when infochemicals are present. Food odours and pheromone thus are able to guide more fruit flies toward the resources.

At the end of the generation, the larvae did not suffer from competition (0% mortality), but instead a high mortality due to the Allee effect occurred. This was the case for all treatments. When both food odours and aggregation pheromone could be used (F+A), the mortality due to the Allee effect in the quadrant with the highest initial density significantly decreased from 84.1% mortality in the control situation and 81.6% for the situation where food is present (F) to 58.8% for F+A (G = 172.1539 (control), G = 159.5866, (F), both p<0.0005). No significant effect is observed in the quadrants with the lower initial population density. As expected, this positive effect is density dependent. When more fruit flies are present, aggregation on the resources can better prevent mortality due to the Allee effect. At the same time no negative effects, like higher mortality due to competition, are observed. By decreasing the mortality in the quarter with the highest initial density, the presence of both food odours and aggregation pheromones thus have an overall positive effect on population numbers. As a result the total number of larvae that survive go up from 677 (control) and 854 (F) to 1757 new adults (F+A) in the whole domain in the next generation.

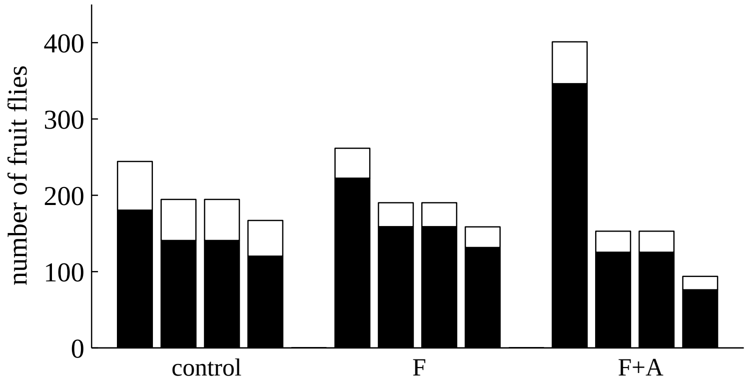

Figure 4 The distribution over the quadrants of the total fruit fly population, subdivided in settled (black part) and leaving (white part) fruit flies, after one generation, for the simulations: without chemical information present (control), with only food odours present (F) and with both food odours and aggregation pheromone present (F+A). Within a treatment, the first bar depicts the quadrant with the highest initial adult population. The second and third bar depict the quadrants positioned adjacent to it, and the forth bar depicts the quadrant positioned opposite to it.

2.3.2 Long term (ten generations) simulation

2.3.2.1 Large spatial scale: quadrants of the domain

The effect of infochemicals on the distribution of the modelled fruit flies depends on resource density. All simulations show a strong increase in population numbers in all 4 quadrants in the first five generations (Fig. 5). In these generations the population is expanding, both spatially and numerically. Because more apples can provide more food for the larvae, the total number of fruit flies increases faster for higher resource density. The presence of infochemicals had a positive effect on population numbers. The mortality due to the Allee effect was significantly lower when infochemicals were present for all resource densities ($p<0.0001$ for both F and F+A).

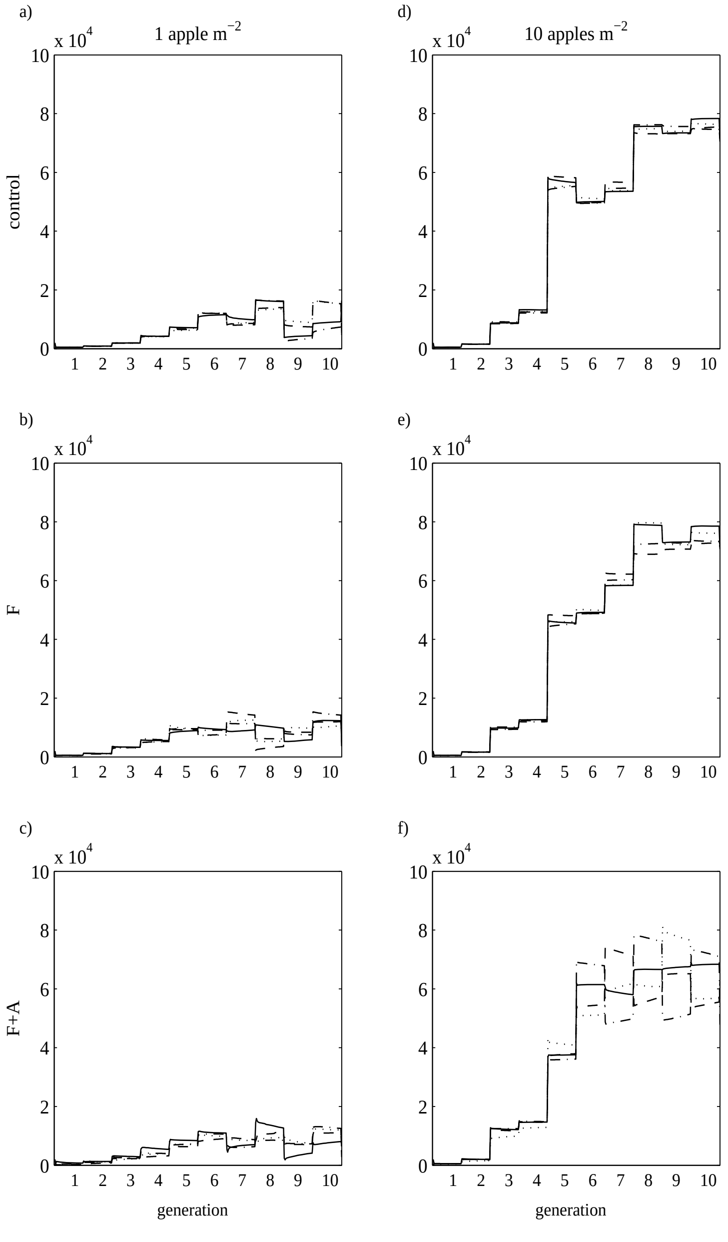

Figure 5 The dynamics of the total number of fruit flies in the 4 quadrants of the domain (each line represents one quadrant) during 10 generations, when no chemical information is present (control), only food odors are present (F) or both food odors and aggregation pheromones are present (F+A), for the resource densities of 1 apple m^{-2} (a-c) and 10 apples m^{-2} (d-f). The apples were randomly distributed per resource block. The initial fruit fly population $H_0 = 2000$ was situated in one cell in the center of the domain. The attraction towards infochemicals was $\kappa = 5$ and $\eta = 2.51$.

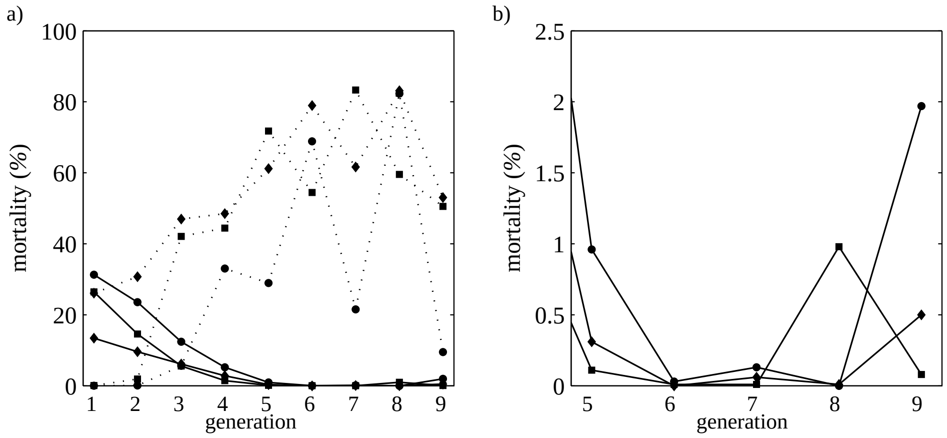

Fig. 6 Larval mortality due to the Allee effect (solid lines) and competition (dotted lines) for (a) all generations, and (b) focused at the Allee effect from the fifth generation onwards, for the control simulation without odors (●), for the simulation with only food odors (■), and for the simulation with both food odors and aggregation pheromone present (♦), for resource density 1 apple m^{-2}. Note the scale difference of the y-axes.

However, at a resource density of 1 apple m^{-2} the presence of infochemicals also caused higher mortality due to competition ($p<0.0001$ for both F and F+A) (Fig. 6a). Even though the increase in mortality due to competition was larger than the decrease in mortality due to the Allee effect, the number of offspring that survived was higher in the presence of infochemicals. Thus, the presence of food odours and aggregation pheromone had a net positive effect on population numbers.

In the first 5 generations, during population growth, there was a significant trend in time, i.e., the mortality due to the Allee effect decreased significantly and mortality due to competition increased significantly (both $p < 0.0001$) (Fig. 6a). This was the case for all treatments (control, F and F+A) and for all simulated resource densities. The fixed factor "generation × treatment" interaction was also significant ($p < 0.0001$) for the mortality due to the Allee effect and due to competition, indicating that even though the mortality in all treatments show a trend in time, the mortality due to the Allee effect remained significantly lower and the mortality due to competition remained significantly higher when infochemicals were present than when fruit flies could not respond to odours.

The population dynamics from the sixth generation onwards is influenced by the resource density. At a resource density of 1 apple m^{-2} large fluctuations in population numbers between generations can be seen for all treatments (Fig. 5a-c). At this resource density, a relatively large number of fruit flies in one generation is generally followed by much lower number in the next generation. Food odours and aggregation pheromone influence the recovery of the population. When no chemical information is present, a high mortality due to competition (> 80%) is usually followed by a slow increase in population numbers due to higher mortality due the Allee effect in the following generation (Fig. 6b). When infochemicals are present, the population increases much faster after a local population crash, because the mortality due to the Allee effect in the following generation is lower when infochemicals were present (Fig. 6b). This was consistent in all repetitions. Attraction toward infochemicals, and thereby decreasing the mortality due to the Allee effect, thus seems to have a stabilizing effect at this resource density. Despite this stabilizing effect the local population dynamics are inherently unstable at this resource density. The fluctuations are in the same order of magnitude as the mean population density.

At a resource density of 10 apples m^{-2} the presence of infochemicals increases spatial variation in population numbers, but also the variation between generations (Fig. 5 d-f). The attraction toward food odours and aggregation pheromone results in a more aggregated distribution. Where the number of eggs produced at the apples exceeds the local larval carrying capacity more often, which results in higher mortality due to competition (83%-87%). At a resource density of 10 apples m^{-2}, the increase in variation between generations (for F+A) did not affect the overall stability and persistence of the population. The fluctuations are much smaller than the mean population density. However, also when fruit flies could not respond to infochemicals, the larval carrying capacity was exceeded considerably. The mortality due to competition varied between 80 and 85%. Generally, for mortality between 80-85%, the population size remained constant, the population decreased when mortality is higher than 85% and increased when mortality is lower than 80%.

At a resource density of 5 apples m^{-2}, the population dynamics show a combination of the dynamics at higher and lower resource densities. The dynamics show large fluctuations, and there is more spatial variation when chemical information is present (Supplementary material: spatial distribution mortality due to Allee effect and competition for 1) control simulation and 2) F+A).

2.3.2.2 Intermediate spatial scale: on and around resource patches

At the scale of resource blocks, the effect of infochemicals in the first five generations is dependent on the distance between the resource block and the initial population. Infochemicals have a positive effect on the survival of the population at the resources close to the initial population. Infochemicals attract more fruit flies toward the resources and thus reduce the Allee-effect-dependent mortality. However, arresting more fruit flies at resources close to the initial population also implies that fewer fruit flies dispersed to more remote resources, resulting in a higher mortality due to the Allee effect at resources further on. In addition, the stronger attraction toward resources close to the release point also causes overcrowding at these resources, and thus higher mortality from competition. However, the positive effect of locally reducing the mortality due to the Allee effect has a greater effect on total population numbers than the negative effect of increased competition. At the large scale, we have found that infochemicals have a net positive effect on the population numbers by decreasing the mortality due to the Allee effect in the first four generations. From the fifth generation on, the negative effects of increased competition have a larger effect on population size than the positive effects of a decrease in mortality due to the Allee effect.

2.3.2.3 Small spatial scale: individual apples

Figure 7 depicts the long term population dynamics of the total population per apple in block one of quadrant one when both food odours and aggregation pheromone are present. At the smallest simulated scale of individual apples the population dynamics in the first four generations exhibits a similar pattern for all apples in one resource block. However, there exists variation in the number of fruit flies present per apple. From the fifth generation on, the population dynamics vary between apples. This variation is mainly caused by differences in the number of fruit flies present in the beginning of the generation. In an area where relatively more fruit flies survived the previous generation, generally, the number of fruit flies on an apple decreased, while apples in an area with low numbers of fruit flies at the start of the generation generally attracted fruit flies. The fruit flies thus tend to distribute more evenly at the end of the generation (for instance look at generation 5 or 9 in Fig 7). This can imply that fruit flies are more attracted to intermediate concentrations of aggregations pheromones than to high concentrations. If this is the case, this would be a good strategy since the survival curve of the larvae is hump-shaped, with the highest survival at intermediate larval densities (Rohlfs and Hoffmeister, 2003).

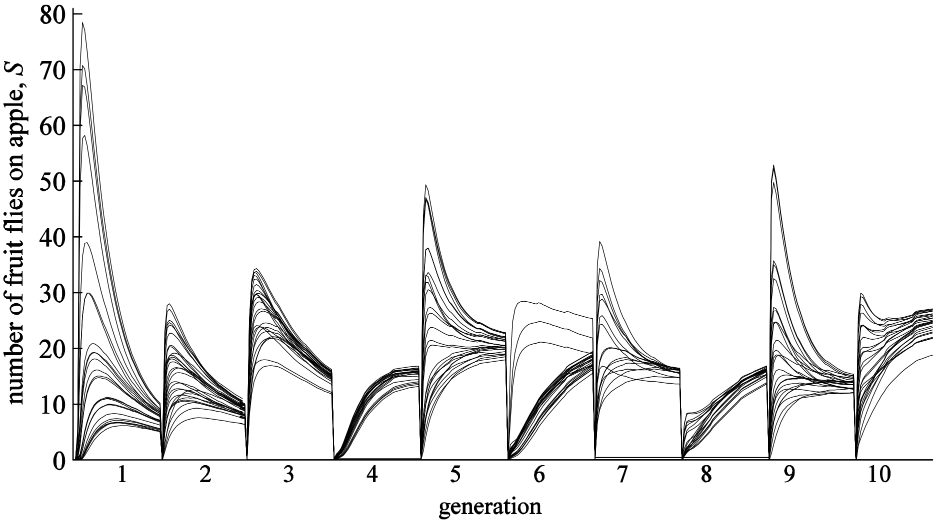

Figure 7 The dynamics of the total number of fruit flies depicted per apple for the resource block closest to the initial population, during 10 generations when both food odors and aggregation pheromone are present (F+A) at resource density 1 apple m^{-2}.

2.4. Conclusion and discussion

We developed a spatio-temporal model for the dispersal of food odours and aggregation pheromone and the responses of a fruit fly population to these infochemicals. In this model, we divided the population in three activity states: individuals could be searching for a resource, be settled on a resource or moving away from a resource. We studied the effect of the presence or absence of food odours and aggregation pheromone on the spatial distribution of a fruit fly population. Furthermore, we investigated the positive and negative effects of the use of infochemicals on population numbers, by looking at larval mortality due to an Allee effect and competition and the net effect on population numbers. We showed that the presence of infochemicals affects the spatial distribution of a modelled fruit fly population. The short term simulations showed that infochemicals guide the flies toward the resources. As expected, aggregation pheromone in combination with food odours caused a higher settlement than food odours alone. Furthermore, the presence and use of infochemicals positively affected the net larval survival (in numbers), by decreasing mortality due to an Allee effect during the colonization of the domain. The effect of infochemicals depended on the distance from the initial population. In accordance to field data of Wertheim et al. (2002), infochemicals attracted more fruit flies toward the resources close to the release point and hereby positively influenced population numbers in the next generation by reducing the mortality due to the Allee effect at these resources.

The use of infochemicals has both positive and negative effects on population size. During the colonization of the domain the positive effects, of a decreased mortality due to the Allee effect, are larger than the negative effects of an increased mortality due to competition, resulting in a stronger population growth when infochemicals are present. After the colonization of the domain and the strong population growth, the negative effect of increased competition is not balanced by a reduced mortality due to the Allee effect anymore, resulting in higher population numbers when no infochemicals are present.

The effect of infochemicals also interacted with the resource density. At a low resource density (1 apple m^{-2}) the presence of chemical information increases the resilience of the system, because it reduces the mortality due to the Allee effect after a population decline due to competition. At high resource densities, the presence of infochemicals increases both spatial and “between-generation” variation, causing large amplitude variations in population sizes. However, due to the higher population densities, these variations pose no threat for population persistence.

The study of Etienne et al. (2002) showed that local instability could be balanced by dispersal and suggested that attraction to infochemicals could be a stabilizing factor for population persistence. Although the population was inherently unstable at a low resource density (1 apple m^{-2}), our long term simulation indeed showed that infochemicals increased population’s resilience, by decreasing the mortality due to the Allee effect after a local population crash, and thus promoted population persistence. Looking at population dynamics at a smaller scale, local instability (at the scale of recourse blocks) in our model was also balanced by dispersal. Apples within a resource block showed similar population dynamics. However, at the scale of resource blocks there was variation in dynamics. This was mainly caused by initial differences in population density due to the rate of colonization and the differences in resource density between generations.

In our long term simulation the initial population was released from one point in the centre in the domain. This is typical for a field experiment but very unrealistic for the natural situation. *Drosophila melanogaster* cannot survive the winter in the natural climate of the Netherlands. Therefore, at the beginning of the season, no natural fruit fly population is present in orchards. Adult *D. melanogaster* overwinter in human constructions (Boulétreau-Merle et al., 2003). They recolonise the orchards from the boundaries in spring. During recolonization, locating the resources, and thus guidance of the fruit flies by infochemical information is important. By placing the initial population in the centre of the domain, close to suitable substrates, the results we found for the growth of the population that could not use infochemicals is probably much better than in the natural situation where the fruit flies had to recolonise the area. In the latter situation, population size is small and the population is also distributed more randomly. Therefore, mortality due to the Allee effect plays a more prominent role. Our results could thus be an underestimation of the positive effect of infochemicals of reducing the mortality due to the Allee effect during population growth. Still, we showed that even under these favourable conditions, the use of chemical information had a positive effect on population numbers during the colonization of the domain. We plan to study the role of infochemicals on long term population dynamics when fruit flies have to re-colonize an orchard in the future.

Studies of Kellogg et al. (1962) and Frye et al. (2003) show that for *D. melanogaster* visual cues are essential to locate the horizontal position of an odour source. In our model, *D. melanogaster* can only use chemical information to find a resource. They use a concentration gradient to find the odour source. This works sufficiently while the odour concentration is lower than the saturation level. However, the moment the odour concentration reaches saturation level our simulated fruit flies cannot locate the resource anymore and start to disperse randomly. In addition, in our model, settlement is dependent on the odour concentration above a resource. As we model in 2D, it is not possible to determine whether the odour originated from that resource or another resource nearby. Yet, an experimental study showed that *Drosophila melanogaster* is able to follow an odour trace to its source (Budick and Dickinson, 2006). Both saturation and the inability to localize the actual odour source could be an explanation for the even distribution of fruit flies over the apples within a resource block we found in our small scale simulation. As both effects could cause a more even distribution, the negative effects of aggregation, in particular, higher mortality due to competition, could be underestimated. However, more competition would also result in lower population numbers. In that case the positive effect of infochemicals by decreasing mortality due to the Allee effect is again more important.

The use of infochemicals thus has not solely positive effects. Infochemicals guide fruit flies toward the resources and thereby can have a positive effect on population numbers by decreasing the mortality due to the Allee effect. On the other hand, when too many fruit flies are attracted, the carrying capacity of an apple can be exceeded which will result in a higher larval mortality due to competition for food. Hoffmeister and Rohlfs (2001) experimentally showed that fruit flies often misjudge the carrying capacity of resources and not only aggregate their eggs when confined to a limited amount of resource items (when it would be appropriate) but also when resources are not a limiting factor. They gave as a possible explanation that ample supply of food patches is not found in nature, and thus that the reproductive success of fruit flies is mainly determined by their opportunities of producing clutches (i.e., locating patches) rather than optimal egg-laying decisions. In a low maintenance orchard in the Netherlands, the density of apples on the orchard floor is 0-6 apples m^{-2} (Wertheim et al., 2006). This is comparable with our simulation with 1 apple m^{-2}. In this simulation infochemicals indeed had a positive effect on the resilience of the population

A mechanism by which aggregation can be advantageous is that at high population densities individuals can experience a diluted risk of attacks by their natural enemies (Parrish and Edelstein-Keshet, 1999; Wertheim et al., 2005). Rohlfs and Hoffmeister (2004) indeed show that risk of parasitism can decrease with increasing larval density. The most important natural enemies of *Drosophila* in temperate regions are their larval parasitoids (Janssen et al., 1988). Wertheim et al. (2006) found that the overall percentage of parasitism in the field by *Leptopilina* spp. on *Drosophila* species in apples was 22%. The percentage of apples that contained *Leptopilina* was even higher, namely 67%. *Leptopilina* spp. use the same odours as fruit flies (i.e., food odours and *D. melanogasters'* aggregation pheromone) to find their hosts (Wiskerke et al., 1993; Wertheim et al., 2003). Parasitism could have a stabilizing effect on the population dynamics of the fruit flies, by decreasing population growth, and thus decreasing the probability of over-aggregation at low resource densities. We suggest that a reduced risk of parasitism in higher larval densities in combination with the use of aggregation pheromones promotes persistence of the host-parasitoid interaction. In future research, we investigate the role of infochemicals in spatial host-parasitoid interactions.

In nonsocial arthropods, hundreds of species belonging to more than ten different orders are known to use aggregation pheromones (Wertheim et al., 2005). Many of these are pest species. Wertheim et al. (2005) found that, generally, there is a connection between aggregation pheromones usage and food exploitation. Knowing the effects of the use of infochemicals on spatial population dynamics of the pest species, if possible in combination with the dynamics of its natural enemy, may lead to novel insights for biological control. Many animal species (but also plant species) suffer from a decrease in growth rate at small population sizes, known as the Allee effect. In these species, the ability to use chemical information, especially aggregation pheromones, enhances population persistence. We found that infochemicals mainly had a net positive effect on population size and population persistence in situations where resources are scarce or difficult to find or when the (local) population of fruit flies is small. This is the case in spring when the natural population that overwintered in shelters recolonises an orchard. We showed that aggregation promotes population resistance during colonization of the domain and, for low resource densities, also for recolonization after a local population crash. Aggregation then decreases the mortality due to the Allee effect. At high resource densities and large population numbers, the use of aggregation pheromones had a net negative effect on population numbers. However, for the persistence of a population the reduction of the larval mortality due to the Allee effect at low population densities was of great importance. At the same time, the negative effect of infochemicals on population numbers due to increased competition at large population size did not have a negative effect on population persistence. Overall, the use of food odours and aggregation pheromones enhances the persistence of a fruit fly population.

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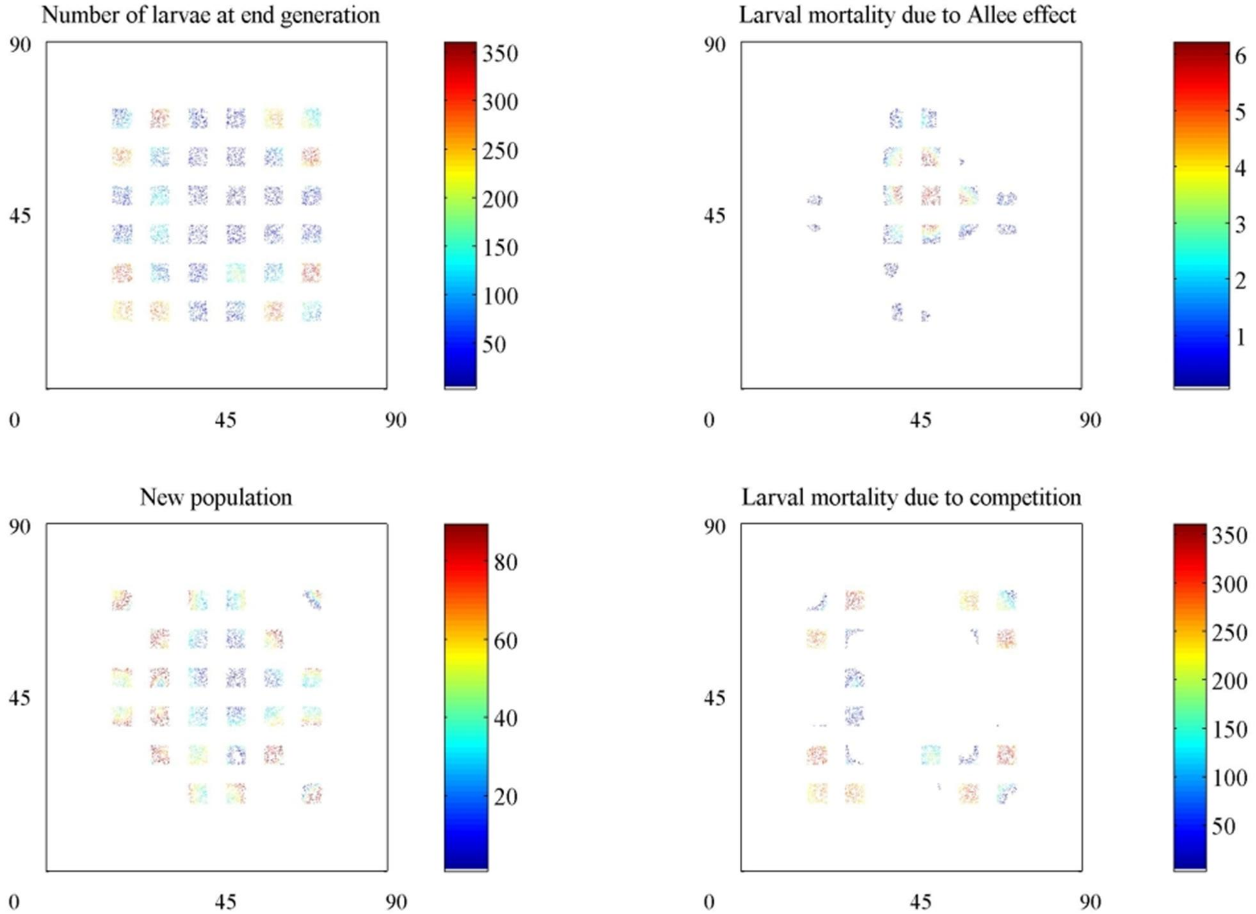
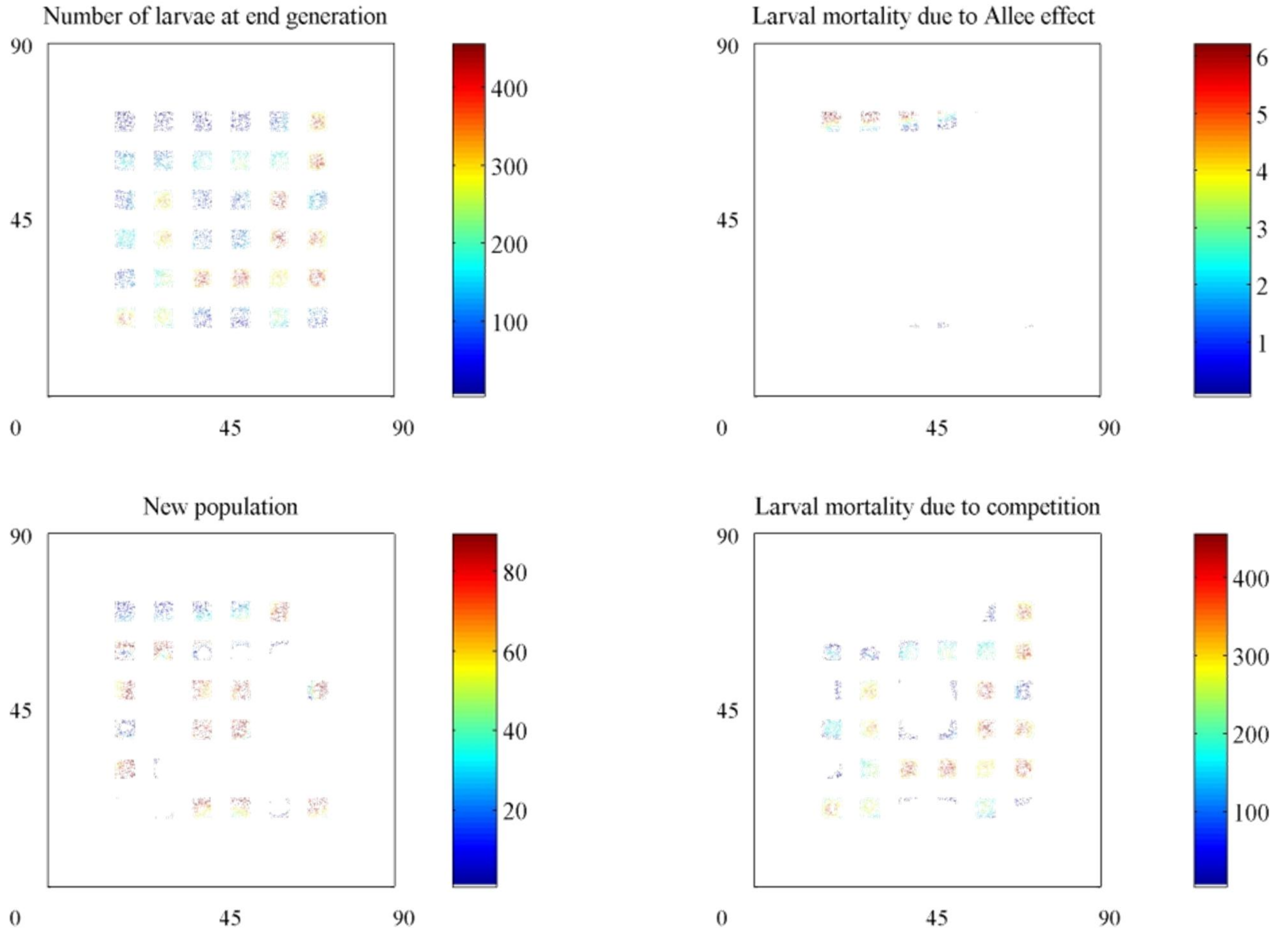
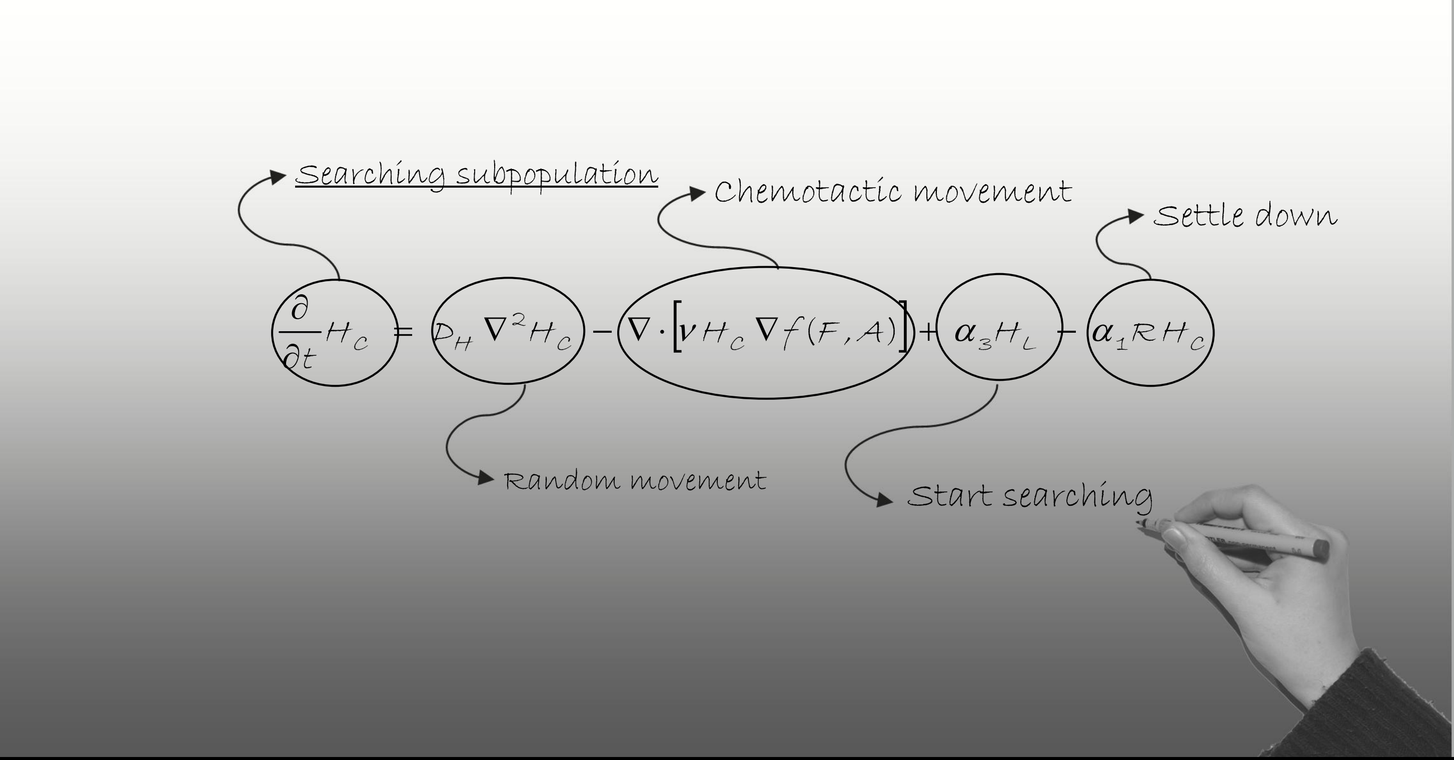


Supplementary material 1 Spatial distribution of the larvae of the fruit fly at the end of the 10th generation (upper left graph), and the density dependent mortality due to the Allee effect (upper right graph) for low larval densities and due to competition for high larval densities (lower right graph) and the resulting new female population (lower left graph) when fruit flies cannot respond to chemical information and thus disperse randomly. The resource density was 5 apples m^{-2}. The attraction towards infochemicals was $\kappa=0$ and $\eta=0$

Supplementary material 2 Spatial distribution of the larvae of the fruit fly at the end of the 10th generation (upper left graph), and the density dependent mortality due to the Allee effect (upper right graph) for low larval densities and due to competition for high larval densities (lower right graph) and the resulting new female population (lower left graph) when fruit flies can respond to chemical information. The resource density was 5 apples m^{-2}. The attraction towards infochemicals was $\kappa=5$ and $\eta=2.51$



Chapter 3



Picture Jasper Blok

The effect of chemical information on the spatial distribution of fruit flies

II Parameterization, calibration and sensitivity

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Abstract

In **Chapter 2** (Lof et al., 2008), we describe a spatio-temporal model for insect behaviour. This model includes chemical information for finding resources and conspecifics. As a model species, we used *Drosophila melanogaster*, because its behaviour is documented comparatively well. We divide a population of *Drosophila* into three states: moving, searching, and settled. Our model describes the number of flies in each state, together with the concentrations of food odour and aggregation pheromone, in time and in two spatial dimensions. Thus, the model consists of 5 spatio-temporal dependent variables, together with their constituting relations. Although we tried to use the simplest submodels for the separate variables, the parameterization of the spatial model turned out to be quite difficult, even for this well studied species. In the first part of this paper, we discuss the relevant results from the literature, and their possible implications for the parameterization of our model. Here, we focus on three essential aspects of modelling insect behaviour. First, there is the fundamental discrepancy between the (lumped) measured behavioural properties (i.e., fruit fly displacements) and the (detailed) properties of the underlying mechanisms (i.e., dispersivity, sensory perception, and state transition) that are adopted as explanation. Detailed quantitative studies on insect behaviour when reacting to infochemicals are scarce. Some information on dispersal can be used, but quantitative data on the transition between the three states could not be found. Second, a dose-response relation as used in human perception research is not available for the response of the insects to infochemicals; the behavioural response relations are known mostly in a qualitative manner, and the quantitative information that is available does not depend on infochemical concentration. We show how a commonly used Michaelis–Menten type dose-response relation (incorporating a saturation effect) can be adapted to the use of two different but interrelated stimuli (food odours and aggregation pheromone). Although we use all available information for its parameterization, this model is still overparameterized. Third, the spatio-temporal dispersion of infochemicals is hard to model: Modelling turbulent dispersal on a length scale of 10 m is notoriously difficult. Moreover, we have to reduce this inherently three-dimensional physical process to two dimensions in order to fit in the two-dimensional model for the insects. We investigate the consequences of this dimension reduction, and we demonstrate that it seriously affects the parameterization of the model for the infochemicals. In the second part of this paper we present the results of a sensitivity analysis. This sensitivity analysis can be used in two manners: firstly, it tells us how general the simulation results are if variations in the parameters are allowed, and secondly, we can use it to infer which parameters need more precise quantification than is available now. It turns out that the short term outcome of our model is most sensitive to the food odour production rate and the fruit fly dispersivity. For the other parameters, the model is quite robust. The dependence of the model outcome with respect to the qualitative model choices cannot be investigated with a parameter sensitivity analysis. We conclude by suggesting some experimental setups that may contribute to answering this question.

Keywords Parameterization · Sensitivity analysis · Chemotaxis · Spatial population dynamics · Integro-difference equations

3.1 Introduction

Animal aggregation is a common phenomenon in ecological systems (Parrish and Edelstein-Keshet, 1999; Wertheim et al., 2005). As the individuals can move freely, there must be a clue that guides them to the aggregate, so the individuals must pick up information and respond to it. The sensory cues involved herein can be visual, auditory, tactile or chemical. In insects, chemical information conveyance is important. Insects trying to find a substrate or host plant, use chemical information for long range detection; at smaller distances, sight also becomes important. The infochemicals to which a species reacts can be either substances emitted by its environment, such as food odours and plant volatiles, or substances that the species itself emits, such as aggregation pheromone.

In order to study the implications of infochemical use on the dynamics of a single species within a spatial context, in **Chapter 2** we developed a model (Lof et al., 2008) that incorporates odour dispersion and the responses of organisms, taking *Drosophila melanogaster* as a model organism. As this species has been used as research model in many studies before, its behaviour is documented comparatively well.

In our model, the drosophilid population is divided into three states, according to their activity: a searching state C (with fly density H_C), in which individuals use infochemicals to find a suitable resource, a settled state S (with fly density H_S), in which individuals spend a period of time on a resource, and a leaving state L (with fly density H_L), in which individuals actively move away from the resource. Hence, we have three state variables and three transitions. As the fruit flies use only the lowest layer (say, up to 2 m above ground level), we can model their density as functions that depend on time and two spatial variables. It should be noted that it would be easy to extend the model to three spatial variables; however, this seriously affects the run times for simulations with the model, and thereby its' practical usefulness.

Relevant modelling questions for transitions between states are: (1) In the transition from the searching state C to the settled state S, what is the relative importance of smell and vision on the fruit fly behaviour, and how does this relation vary with the distance to the resource? (2) In the transition from S to the leaving state L, how long do fruit flies remain settled on their resource? and (3) In the transition from L to the searching state C, how long (or how far) do fruit flies fly away from their resource before they start to search for a new resource?

There are also questions about the behaviour of flies in a particular state that require an answer: (4) in the searching state C, how do individuals of *Drosophila melanogaster* search? Can they sample the infochemicals so frequently that they can smoothly follow a concentration gradient, or is the sampling rate so low that their flight pattern consists of connected line segments? And what is their sensory dose-response relation? (5) In the settled state S, the actual population dynamics take place. Here an appropriate model must be chosen, possibly including scramble competition and/or an Allee effect. (6) In the leaving state L, the fruit fly first actively covers some distance from its former resource; but how fast and how far?

There also are the physical laws for the spreading of the infochemicals: (7) how fast are the infochemicals produced, how fast do they evaporate, and how fast do the evaporated infochemicals disperse through the air? Furthermore, there is a difference in the vertical domain for the fruit flies and the infochemicals: whereas the fruit flies use only the lowest layer, a fraction of the infochemicals may disperse higher than this. Therefore (8), we have to estimate at what rate the infochemicals get out of reach. Although we adopted quite basic models to describe these separate processes, there still are a large number of parameters in the resulting model. In the first part of this paper, we discuss how we use data that we found in the existing literature for the parameterization of the model. Despite all performed research, many parameterization questions remain unanswered: the experimental research was simply not aimed at mathematical model building at the level of detail that we aim at. Nevertheless, even with a model in which not all parameters are known, simulations can be done that lead to important ecological results and questions. This is what we set out to do in **Chapter 2** (Lof et al., 2008), where we used the simulations to investigate the possible consequences of infochemicals on the spatial population dynamics. In the absence of a proper parameterization, the inferences are rather qualitative. Therefore, we also performed a sensitivity analysis on our parameter values, which we present in the fourth section of this paper; the results of this analysis can be used to determine the generality of our conclusions also for different parameter values.

3.2. Parameterization of the model: short term dynamics

Our model deals with *Drosophila* fruit flies that have to search for resources (i.e. yeast-infected apples), where they can eat, mate and where females can oviposit. Details of the spatial model structure are given in **Chapter 2** (Lof et al., 2008). In this model, the spatial domain is discretised into patches that can contain a resource item. The short term dynamics of the fruit flies is modelled with the equations (1-8), describing the redistribution of adult *Drosophila* population H over three different states: the searching state (with density of flies H_C), the settled state (with density of flies H_S), and the leaving state (with density of flies H_L).

$$R(x,y) = \begin{cases} 0 & \text{if no apples are present at position } (x,y) \text{ at time } t \\ 1 & \text{if an apple is present at position } (x,y) \text{ at time } t \end{cases} \tag{1}$$

$$\frac{\partial}{\partial t} H_C = D_H \nabla^2 H_C - \nabla \cdot \left[\nu H_C \nabla f(F,A) \right] + \alpha_3 H_L - \alpha_1 R H_C \tag{2}$$

$$\frac{\partial}{\partial t} H_S = \alpha_1 R H_C - \alpha_2 H_S \tag{3}$$

$$\frac{\partial}{\partial t} H_L = \alpha_2 H_S - \alpha_3 H_L \tag{4}$$

$$f(F,A) = \frac{F}{F_0 + F} + \eta \frac{FA}{F_0 A_0 + FA} \tag{5}$$

$$\frac{\partial}{\partial t} F = D_I \nabla^2 F - \mu F + \theta_F R \tag{6}$$

$$\frac{\partial}{\partial t} A = D_I \nabla^2 A - \mu A + \omega A_R \tag{7}$$

$$\frac{\partial}{\partial t} A_R = \theta_A H_S - \omega A_R \tag{8}$$

Here F and A are the concentrations in the air of food odours and of aggregation pheromone, respectively. The amount of aggregation pheromone (in liquid or adsorbed form) at the resource is A_R, and f is a sensory index function with a nonlinear interdependence on both infochemicals, to be explained in Section 2.3. The parameters in these model equations are given in Table 1.

In Eqs. (2)–(8), we did not mention the time and spatial coordinates explicitly, but all dynamic variables depend on time and position: the fly densities H_C, H_S and H_L as well as the infochemical concentrations F, A and the amount of liquid pheromone A_R. Clearly, the settled flies (H_S) can only be present on the resource items. The fruit flies come into the moving state by actively flying away from their resources, but in Eq. (4), it is not stated explicitly how this movement is modelled. In **Chapter 2** (Lof et al., 2008), we assume that the fruit flies actively fly away with a velocity ρ from the resource in arbitrary directions. This process cannot be modelled with ordinary or partial differential equations; in an integro-difference equation it is modelled with a ring random dispersal kernel.

3.2.1 Fruit fly behavioural parameters

Transition rates

No quantitative information is available on the probability that a fruit fly actually settles on a resource after having detected it. Experimental work by Wertheim et al. (2002a) showed that the numbers of fruit flies that settled quickly built up in the first 15 minutes of the experiment, subsequently followed by a more gradual increase up to on average 100 out of the 200–400 released fruit flies. However, it is hard to derive an estimate for a settling rate from their data, because the total number of flies is not exactly known. Nevertheless, the experiment suggests that there is a rather high probability that a fruit fly settles the moment it finds a resource, and we use $\alpha_1 = 0.25\ \mathrm{min}^{-1}$. With this value, 71% of the searching population that found a resource settles within an interval of 5 minutes (this is the time step size in our simulations).

The gradual increase after the quick settlement indicates that fruit flies remained on the resource for a period of time (Wertheim et al., 2002a). Again, we adopt the simplest possible model: the probability of a settled fly leaving the resource per unit of time is constant, not depending on its residence time on that resource or on the local fruit fly density. This proportionality constant must be small as compared to α_1: we take $\alpha_2 = 0.002\ \mathrm{min}^{-1}$. Then in each interval of 5 minutes, 99% of the settled population remains. We further assume that after leaving the resource, fruit flies quickly start searching for a new resource. We choose $\alpha_3 = 0.5\ \mathrm{min}^{-1}$. This means that on average a fruit fly moves away from a resource for 2 minutes, after which it starts to search for a new resource.

Using these parameter values, the fractions of $\underline{H}_C$, $\underline{H}_S$, and $\underline{H}_L$ in equilibrium (in a homogeneous domain) can be calculated. In equilibrium, the time derivatives in (2-4) vanish. In that case

$$\alpha_3 \underline{H}_M = \alpha_2 \underline{H}_R = \alpha_1 \underline{H}_S \tag{9}$$

Using the fact that these fractions add up to 1, we obtain

$$\underline{H}_L = \frac{\alpha_1\alpha_2}{\alpha_1\alpha_2 + \alpha_1\alpha_3 + \alpha_2\alpha_3}, \quad \underline{H}_S = \frac{\alpha_1\alpha_3}{\alpha_1\alpha_2 + \alpha_1\alpha_3 + \alpha_2\alpha_3}, \quad \underline{H}_C = \frac{\alpha_2\alpha_3}{\alpha_1\alpha_2 + \alpha_1\alpha_3 + \alpha_2\alpha_3}. \tag{10}$$

Hence, for $\alpha_1 = 0.25$, $\alpha_2 = 0.002$, and $\alpha_3 = 0.5$, we find that $H_L = 0.004$, $H_S = 0.988$, and $H_C = 0.008$. Thus, in a homogeneous world of suitable substrate, fruit flies would spend 98.8% of their time on the substrates and only 1.2% flying.

As these values hold only for a homogeneous domain, they are not very indicative for the actual proportions. Indeed, when the soil is covered with yeast-infected apples, the necessity for searching is virtually eliminated. In the real world, the resources are scarce and ephemeral; therefore, the above-mentioned percentages are rather unrealistic. As the flies must spend more time searching, the actual value for H_C, is much higher (depending on the resource density), and the values for H_S and H_L are correspondingly lower. If the spatial layout is specified, one may compute the equilibrium fractions by solving the corresponding time-invariant partial differential equations. Based on a few of these

Table 1. The model parameters involved in the short time dynamics and their values as discussed in the text below

Name	Description	Value	Units
D_H	Dispersal coefficient of at random moving fruit flies	0.058	m^2 min^{-1}
α_1	Settlement rate of searching fruit flies	0.25	min^{-1}
α_2	Resource leaving rate of settled fruit flies	0.002	min^{-1}
α_3	Start-to-search rate of leaving fruit flies	0.5	min^{-1}
ρ	Velocity of movement away from the resource	1	m min^{-1}
F_0	Saturation parameter for food odours	10	ng m^{-2}
A_0	Saturation parameter for aggregation pheromone	0.04	ng m^{-2}
D_I	Dispersion coefficient of infochemicals	1	m^2 min^{-1}
$\mu(720)$	Loss rate of infochemicals in a 12 hours period (measured from the moment of production)	0.025	min^{-1}
$\mu(5)$	Loss rate of infochemicals in a 5 minutes period (measured from the moment of production)	0.171	min^{-1}
θ_F	Food odour production by the resource	2	ng apple^{-1} min^{-1}
θ_A	Aggregation pheromone production by settled fruit flies	0.83	ng fly^{-1} min^{-1}
ω	Evaporation rate of liquid aggregation pheromone	4.10^{-4}	min^{-1}
ν	Attraction to infochemicals	$5D_P$	m^2 min^{-1}
η	Attraction ratio of food odour together with aggregation pheromones relative to the attraction to food odour alone	2.51	–

experiments, we estimate that fruit flies spend 70% of their time on the resources and 30% dispersing.

Fruit fly dispersal

Usable data on the mobility of fruit flies are scarce. From the results reported by Timofeeff-Ressovsky and Timofeeff-Ressovsky (1941), we infer that *Drosophila melanogaster* moves 10 m or less per day in the field. As the mean dispersal distance of a two-dimensional random dispersal process is $\surd(\pi D_H t)$, this would indicate a dispersal coefficient D_H = 30 m^2 per day if this displacement could be attributed to a completely random movement of the entire fruit fly population. However, in our model a considerable part of the movement is attributed to active searching, and this reduces the dispersion coefficient. Therefore, a dispersion coefficient D_H = 12.5 m^2 per day for the total population, as adopted by Etienne et al. (2002) seems to be realistic.

The dispersion coefficient D_H = 12.5 m^2 per day relates to the displacement per day for the total population. Since we divided the population into two active states and one static state, the two active states also have to make up for the part of the population that does not disperse. When we estimate that fruit flies spend 70% of their time on the resources and 30% dispersing, the value D = 12.5 m^2 per day for the total population gives

$D_H = 12.5 / 0.3 = 41.7$ m^2 per day for the searching population. With a day length of 12 hours this is equivalent to $D_H = 0.058$ m^2 min^{-1} (Table 1).

Leaving the resource

No information is available on the distance covered by fruit flies between leaving a resource and starting to search actively for a new one. It is obvious that they first have to move actively away from the resource, because a fruit fly that starts searching for a resource as soon as it leaves a resource only has a small probability of not returning to the same resource. We arbitrarily chose a flight speed of $\rho = 1$ m min^{-1}, in a random direction from its leaving point, and a transition rate to the searching state $\alpha_3 = 0.5$ min^{-1}. This implies that the flies fly away from the resource during on average 2 min before they start to search again. During this time, they cover an average distance of 2 m.

3.2.2 Infochemical distribution

Infochemical dispersion

In **Chapter 2** (Lof et al., 2008), we assumed calm weather conditions, that is, no wind (in such weather conditions, the fruit flies are most active). However, even in the absence of an advective wind flow, the air is subject to turbulence. Thus the infochemicals are dispersed randomly, with a turbulent dispersion coefficient (or eddy diffusivity) that is much larger than the molecular diffusion coefficient. (For small molecules in air, the molecular diffusion coefficient is about 10^{-3} m^2 min^{-1}) We studied the dispersion of soap bubbles in a closed room, and estimated that $D_I = 1$ m^2 min^{-1}. Note that for the value of the dispersion coefficient, it is not relevant whether the dispersion process takes place in one, two or three dimensional space.

Infochemical production and emission

Recently mated females emit 300 ng of *Drosophila* aggregation pheromone (*cis*-vaccenyl acetate or cVA) on the substrate in the first 6 hours after mating (Bartelt et al., 1985). This gives an aggregation pheromone deposition on the resource (A_R) of $\theta_A = 0.83$ ng per adult female per minute. Before the pheromone that is deposited at the resource gets available to the searching fruit flies in the air, it has to evaporate first. This evaporation is a very slow process. In a laboratory experiment, Bartelt et al. (1985) found that 31% of the original amount of cVA in a dish was still present after 2 days. We used this figure to estimate the evaporation rate ω of the cVA, assuming a steady linear decay process for the liquid phase (Eq. 11), which results in a value for ω of $1.3 \cdot 10^{-4}$ min^{-1}.

$$\int_0^{2\text{ days}} \omega \exp(-\omega\tau)\, d\tau \;=\; 0.31 \tag{11}$$

It is not very obvious how this laboratory evaporation rate should be transferred to field conditions. Probably, evaporation in the field is considerably faster than in the laboratory, firstly because of the higher turbulence (even without wind), and secondly because of heating by sunlight. On the other hand, however, cooling down at night hampers evaporation. As our model aims to simulate field conditions in daytime hours, we use an evaporation rate that is considerably higher than in the laboratory: $\omega = 4 \cdot 10^{-4}$ min^{-1}. To quantify the production of food odours we chose ethyl acetate as a characteristic food odour. Yeast infected apples produce this chemical and *D. melanogaster* responds to it (Hutner et al., 1937; Echeverría et al., 2003). Echeverría et al. (2003) found that at harvest date, such apples release 4,800 ng ethyl acetate per kg into the air in 8 hours. Assuming there are approximately 5 apples in 1 kg, this gives an emission of food odours of $\theta_F = 2$ ng per apple per minute.

Infochemical loss

Our fruit fly model is essentially two dimensional in space. This implies that the vertical component is ignored. We envision the physical fruit fly habitat as a 2 m thick air layer above ground level, and model the number of flies per unit area of the field. Whereas the flies can be considered to be confined to such a layer, the emitted infochemicals obviously are not. Hence, there is a certain loss of infochemicals as they move upward by dispersion, out of reach of the flies. In this section we discuss this loss rate into the third dimension.

Consider a constant odour source with an emission rate $c(t)$ (ng/min) starting at $t = 0$ at the origin. The amount of odour in a layer with thickness h at time t (in minutes) is

$$Q_{3\mathrm{D}}(t,h) = \int_0^t c(t-\tau)\,\mathrm{erf}\left(\frac{h}{2\sqrt{D_I\,\tau}}\right) d\tau \tag{12}$$

So, for a constant emission rate $c = 1$ (ng/min) starting at $t = 0$,

$$Q_{3\mathrm{D}}(t,h) = \int_0^t \mathrm{erf}\left(\frac{h}{2\sqrt{D_I\,\tau}}\right) d\tau = \left(-\frac{h^2}{2D_I\,t}\,\mathrm{erfc}\left(\frac{h}{2\sqrt{D_I\,t}}\right) + \mathrm{erf}\left(\frac{h}{2\sqrt{D_I\,t}}\right) + \frac{h}{\sqrt{\pi D_I\,t}}\exp\left(-\frac{h^2}{4D_I\,t}\right)\right) t\,. \tag{13}$$

Figure 1 shows the graph of this function for $D_I = 1$ m^2/s and $h = 2$ m, on a time interval of 36 hours. Note that for $c = 1$ the total odour released at time t equals t.

It is clear that for increasing t, there is a quite large and increasing fraction that leaves the layer; initially, however, the loss is quite small. This was to be expected, as the odour is released at the bottom of the layer, and it takes time to get to the boundary at the top of the layer where it can escape. This behaviour is essential for the 3D model, and it cannot be captured in a 2D model. In an attempt to mimic the 3D behaviour as much as possible, we introduce a loss rate for infochemicals in the 2D model. With a loss rate μ, the amount of odour from a source with constant emission rate $c = 1$ (ng/min) starting at $t = 0$ is

$$Q_{2\mathrm{D}}(t,\mu) = \int_0^t \exp(\mu(\tau - t))\,d\tau = \frac{1-\exp(-\mu t)}{\mu}\,. \tag{14}$$

Using a constant (nonzero) loss rate causes the available amount in the 2 m thick layer to be bounded, whereas in the 3D model this amount grows unboundedly as a function of time, see Figure 1. However, for a small time interval, the 2D loss model can approximate the 3D layer model much more accurately (see Figure 2). Given a time interval, we can adapt the loss rate in such way that the time average over that interval for the 2D model with that loss rate and the 3D model both result in the same amount of odour to disappear from the layer (see Figure 3). The resulting function has a maximum approximately at $t =$ 5 min. For larger values, the loss rate must be decreasing to give the proper average value. For $t < 30$ min, the 2D model approximates the 3D model accurately enough. For larger times, the 2D approximation with the loss rate overestimates the total odour amount in the first half of the interval, and underestimates this amount at later times.

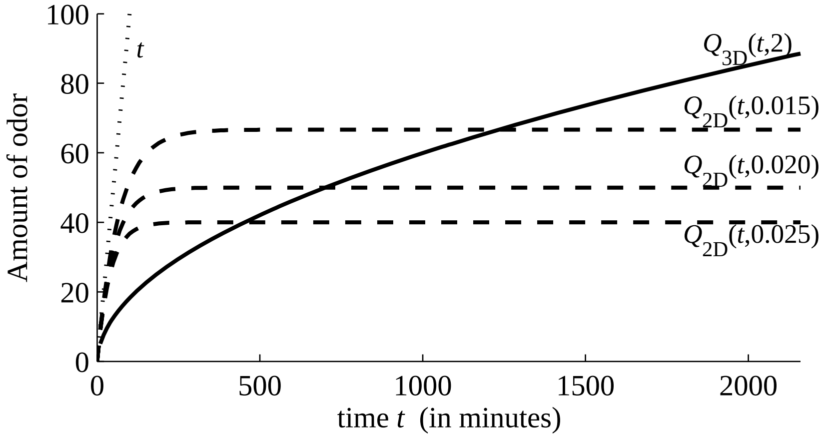

Figure 1. Odour produced by a unit source as function of the time t (in minutes). Dotted line: total amount. Solid line: $Q_{3D}(t, 2)$, amount within a 2 m layer at ground level. Dashed lines: $Q_{2D}(t, \mu)$, amount in a 2D domain with a loss rate μ = 0.015, 0.02 and 0.025 respectively.

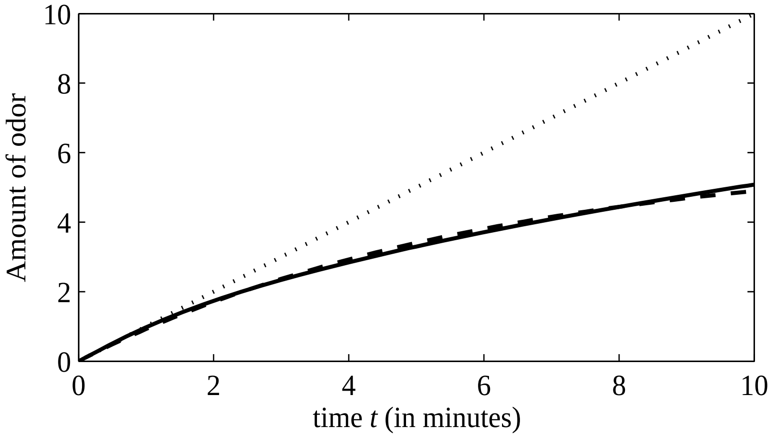

Figure 2. Odour produced by a unit source as function of the time t (in minutes). Dotted line: total amount produced. Solid line: $Q_{3D}(t,2)$, amount within a 2 m layer at ground level. Dashed line: $Q_{2D}(t,0.165)$, amount in a 2D domain with a loss rate μ = 0.165.

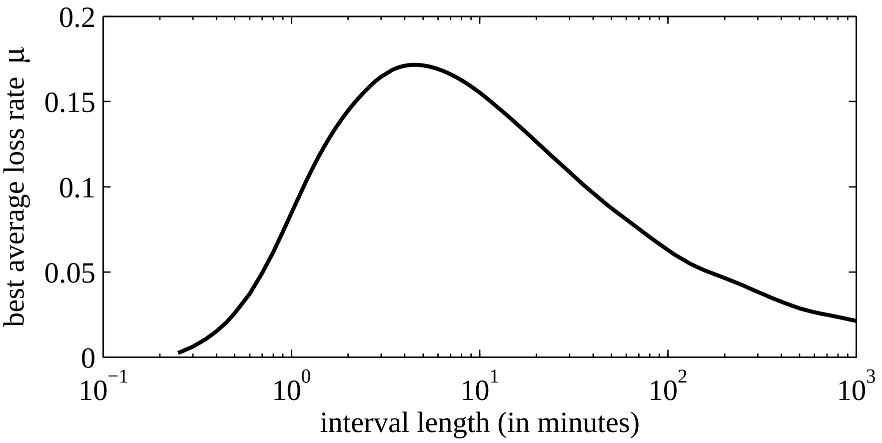

Figure 3. Average loss rate μ, as a function of the length t of the time interval on which it is used.

Typical average loss rates $\mu(\tau)$ are 0.085, 0.165, 0.171, 0.155, 0.109, 0.081, 0.048 and 0.025 min^{-1} for averaging times τ of 1, 3, 5, 10, 30, 60, 180 and 720 min respectively. In our model we used $\mu(5)$ for the recently produced odours and $\mu(720)$ for the odours that were already present in the system. Note that all results depend on the layer thickness h and dispersivity D_I.

3.2.3 Fruit fly response to infochemicals

In modelling the response of fruit flies to infochemicals, the following considerations are taken into account.

1. The strength of smell of the flies depends on the fraction of neuro-receptors that is occupied by infochemical molecules. As the total number of receptors is finite, this implies that there is a saturation effect at high levels of infochemical concentration, which can be represented by a Michaelis–Menten type of response (Postma, 2003).
2. Fruit flies react on food odours and aggregation pheromone in a rather complicated way. Bartelt et al. (1985) showed that for *D. melanogaster*, the aggregation pheromone is only attractive when food odours are also present; and that the combination of food odours and its aggregation pheromone is about four times more attractive than food odours alone.

Although many sensory response functions are conceivable that are consistent with these considerations, functions that depend only on a linear combination of the concentrations are not among these. A simple relation that is consistent with these findings is given in Eq. (5). In adopting a sensory response relation, we assume that the fruit flies' sense of direction does not depend on the actual concentration gradients of the infochemicals, but rather on how the fruit flies perceive this gradient. For a relation as Eq. (5), the effect of this assumption is manifest especially at high concentration levels, in the saturation region of the Michaelis–Menten equation. There, the differences in response to concentrations may become so low that the smell loses its direction.

Attractiveness of infochemicals and attraction ratio

The attractiveness of infochemicals (ν) is a parameter that quantifies the directionality of the movement. Instead of parameterising ν directly, we use $\kappa = \nu/D_H$ as characteristic ratio between the random motion and the active search motion: when $\kappa = 0$, movement is random, and the higher the value of κ, the more the movement is directed toward the odour source. No specific estimate was available for the attractiveness of infochemicals for *D. melanogaster*. Powell et al. (1998) used $\kappa = 10$ for mountain pine beetles. As the population dynamics in our system take place at a smaller spatial scale than the dynamics of the mountain pine beetle, we assumed that κ would be smaller, too. We arbitrarily chose $\kappa = 5$.

Bartelt et al. (1985) showed that after 3 minutes in a wind tunnel, about four times more adult *D. melanogaster* were attracted by the combination of food odours and the aggregation pheromone than by food odours alone. In a field experiment, Wertheim et al. (2006) found after 10 minutes a 1:4.5 ratio of fruit fly numbers on substrates with food odour only (F) and food odour combined with aggregation pheromone (F+A), respectively. These results are very alike. We used Wertheim's 1:4.5 ratio in combination with our chosen κ to estimate the attraction ratio η. Therefore we set up a simulation on a 2D domain similarly sized as Wertheim's field experiment, with four F resources containing only apple-yeast mixture, and four F+A resources, containing an apple-yeast mixture with 4,500 ng synthetic pheromone evaporating at a rate of $\omega = 4 \cdot 10^{-4}$ min^{-1}. Thus, we have a pheromone emission rate of 18 ng min^{-1}. The resources were placed in two rows of four, at regular intervals in alternating order (3 m between rows and 2 m between resources in a row).

The initial adult population is homogeneously distributed. We ran the simulation for 10 minutes, with time steps of 0.25 minute, for varying values of η and for varying values for the production of food odours. Figure 4 shows (for $\kappa = 5$) the values for η corresponding to a 1:4.5 ratio for the average number of fruit flies on the two types of resources for various values of the food odour production. There is a minimum value for $\eta = 2.5$ for which the experimental results of Wertheim can be reproduced, at a food odour production of 2.5–3 ng per resource per minute. For all other values of food odour production, the value of η must be taken higher.

By coupling κ and η, we kept the attraction ratio constant (at 1:4.5) and, therefore we could study the sensitivity of the model for our chosen κ on its own. In our sensitivity analysis we simulated for $\kappa = 2.5$ with $\eta = 5$ and for $\kappa = 7.5$ with $\eta = 1.67$.

Half saturation value for aggregation pheromone and food odour

Wertheim et al. (2006) studied the dose response relation of *D. melanogaster* for cVA. We used their Fig. 1e to calculate the half saturation value of pheromone. This figure depicts the average number of fruit flies found on substrates containing four different doses of cVA (q = 0, 0.45, 4.5 and 45 µg). The number of fruit flies was counted every 10 minutes for 3 hours. We used nonlinear regression to estimate the half saturation value (q_0), using the Michaelis-Menten equation as model,

$$H = H_0 + \frac{bq}{q_0 + q} \tag{15}$$

where H_0 is the number of settled fruit flies settled on substrates without aggregation pheromone, and b is a parameter describing the increase in number of fruit flies due to the presence of aggregation pheromone. We found $q0 = 3.5$ µg (with $H_0 = 8.5$ and $b = 18.2$) as the best solution.

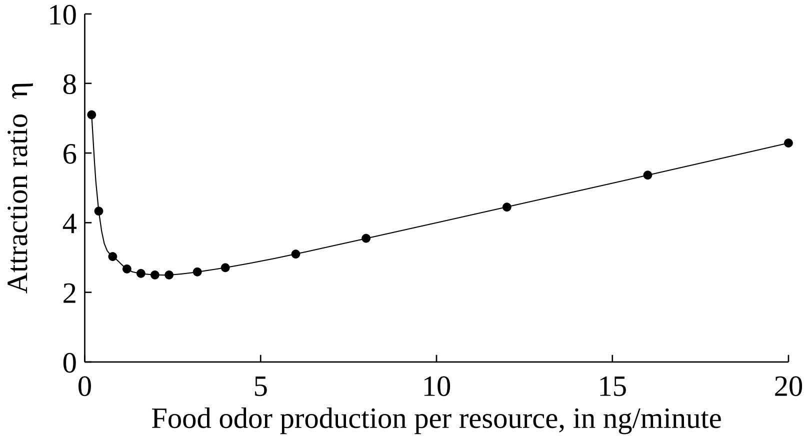

Figure 4. The combination of pheromones and food odour is 4.5 times as attractive as food odour alone. The corresponding value of η depends on the food odour concentration.

Again, we translate this into concentrations of volatile compounds in the air. Using the previously derived evaporation rate $\omega = 4 \cdot 10^{-4}$ min^{-1}, we approximate the emission rate as $q_0\omega$ in the transient phase (up to one day). If the pheromone spreads by a 3D dispersion process, then its concentration at distance r from the source is

$$u(r,t) \;=\; q_0\,\omega \int_0^t \frac{\exp(-\frac{r^2}{4D\tau})}{(4\pi D\tau)^{3/2}}\,d\tau\,. \tag{16}$$

The length scale of the experiments of Wertheim et al. (2006) was 2 m, and saturation effects were observable after 20 minutes. Therefore, we assume that the A0 value as calculated in Eq. (17) is an indication of the half-saturation value for pheromone:

$$A_0 \;=\; u(2,10) \;=\; q_0\,\omega \int_0^{10} \frac{\exp(-\frac{4}{4D\tau})}{(4\pi D\tau)^{3/2}}\,d\tau \;=\; 4.2\cdot 10^{-5}\ \mu\text{g}/\text{m}^3 \tag{17}$$

3.3. Parameterization of the model: long term dynamics

3.3.1 Between-generation dynamics: reproduction and survival

Adult females that have settled on a resource (H_S) deposit on average ξ eggs per minute. The cumulative number of eggs (N) on each resource item after three days (in generation n) is, therefore,

$$N(x,y,n) \;=\; \int_0^3 \xi\, H_S(x,y,n)\,dt\,. \tag{18}$$

Due to the Allee effect and scramble competition, the probability of successful larvae development depends on the number of larvae and, therefore, on N. Hence, the next female population has density $H(x, y, n+1)$,

$$\begin{gathered} H(x,y,n+1) \;=\; \varphi\, N(x,y,n)\, s_A(N)\, s_C(N)\,, \\ s_A(N) \;=\; \frac{1}{1+e^{-c_A(N-N_A)}}\,, \quad s_C(N) \;=\; \frac{1}{1+e^{c_C(N-N_C)}} \end{gathered} \tag{19}$$

where $s_A(N)$ and $s_C(N)$ model the reduction of the larvae survival rate because of the Allee effect and the scramble competition, respectively. The sex ratio φ is the fraction of females in the larval population.

3.3.2 Fecundity

A study of Boulétreau (1978) showed that *D. melanogaster* has a mean fecundity of 6 eggs per day in the field. As we use a day length of 12 hours in our simulations, we set ξ = 6 eggs per 720 min = 0.0083 eggs min^{-1}.

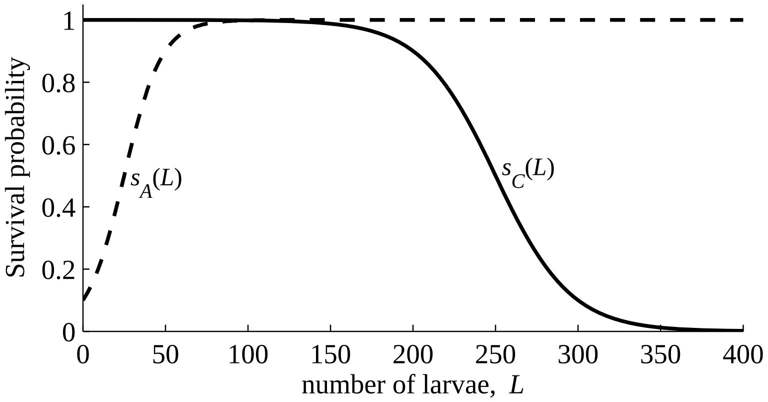

Figure 5. Larval survival probabilities as functions of the number of larvae on a resource item. The dashed line shows the larval survival related to the Allee effect (s_A), the solid line gives larval survival related to competition (s_C), as given in Eq. 19.

Table 2. The model parameters involved in the reproduction dynamics.

Name	Description	Value	Units
ξ	Fecundity of the settled population	0.0083	min^{-1}
φ	Sex ratio of the larvae (fraction of females)	0.5	–
N_A	Number of larvae per apple at which 50% survives the Allee effect	25	–
N_C	Number of larvae per apple at which 50% survives competition	250	–
c_A	Slope sigmoid survival curve modeling the Allee effect	0.088	–
c_C	Slope sigmoid survival curve modeling the competition	0.044	–

3.3.3 Larval survival

The larval survival probability is modelled with the sigmoid functions $s_A(N)$ for the Allee effect and $s_C(N)$ for the competition, both of which contain two parameters. In the model, we use yeast-infected apples as the substrate for larval development. One apple can support development of at most 200-300 *D. melanogaster* larvae (Sang, 1956). We assume that in the interval (200, 300) competition reduces larval survival approximately from 90% to 10%, see Figure 5. This implies 50% survival at $N_C = 250$ larvae and a slope $c_C = 0.044$.

For the Allee effect, no quantitative data were found in literature. An indication can be found in Rohlfs and Hoffmeister (2003), who observe a high mortality at low larval densities. Therefore, we (arbitrarily) choose 50% survival at $N_A = 25$, increasing to 90% survival at 50 larvae see Figure 5; this implies a slope $c_A = 0.088$.

3.4. Sensitivity analysis

The primary state variables of our model are the three functions of time and position $H_C(t, x, y)$, $H_S(t, x, y)$, $H_L(t, x, y)$, modelling the density of searching, settled and moving fruit flies, respectively. Since the output of the model contains many data, there are numerous ways to measure and weigh the effects of a parameter change in the model. As described in **Chapter 2**, the model was tested on several time scales: the short term (up to one generation), and the long term (from one to ten generations). It turned out that the long term dynamics displays a chaotic pattern (see **Chapter 2**, Fig. 7). This behaviour is caused by the counteracting effects of the competition and the Allee effect, and it is persistent over a wide range of parameters. Therefore, a sensitivity analysis is not very useful in this situation: the qualitative result, displaying chaotic oscillations, is quite robust, but the quantitative result at any point in time and space may depend critically on the parameter values (and initial conditions).

At the short term, a sensitivity analysis is much more useful. It enables us to investigate how the changes in the parameters of the model affect the fruit fly behaviour, especially with respect to its success rate in finding a suitable resource. For this sensitivity analysis, we ran one day simulations as described in **Chapter 2**, on a symmetric field, starting with 500 flies in the first quadrant, and 100 flies in each of the other three quadrants. For output variables we compared using the default parameter value and two alternative values, (1) the total number of flies in the first quadrant, $H_{\mathrm{tot},1}(t)$, may decrease by dispersion and increase by chemotactically induced aggregation. Therefore, this number acts as an indication of the relative strength of these two opposite effects; and (2) the number of settled flies in the first quadrant, $H_{R,1}(t)$. This number gives an indication of the success in finding resources.

Both $H_{tot,1}(t)$ and $H_{S,1}(t)$ may be used as indicators for aggregation, $H_{tot,1}(t)$ on a larger spatial scale than $H_{S,1}(t)$. We compared $H_{\mathrm{tot},1}(t)$ and $H_{S,1}(t)$ for the different parameter values in two manners: (1) a qualitative comparison of the behavioural dynamics curves of $H_{\mathrm{tot},1}(t)$ and $H_{S,1}(t)$ on the interval $0 \leq t \leq 12$ hr, and (2) a quantitative comparison of the final values $H_{\mathrm{tot},1}(12\mathrm{hr})$ and $H_{S,1}(12\mathrm{hr})$.

3.4.1 Fruit fly behavioural parameters

Transition rates: α_1, α_2, α_3

The settlement rate α_1(with standard value 0.25 min^{-1}) has been varied from 0.125 to 0.375 min^{-1}. This causes the settlement after 5 minutes to vary from 46.5% to 84.7%, and affects the distribution over the states through the settled population (Table 3). As expected, the settled population increases with an increasing settlement rate.

The model is most sensitive for the patch leaving rate α_2. Varying α_2 (with standard value 0.002 $\mathrm{min}–^{1}$) between 0.001 and 0.003 $\mathrm{min}–^{1}$ causes a fraction from 0.5% to 1.5% of the settled population to leave the resource within 5 minutes. Increasing α_2 impedes the growth in the number of settled adults considerably over the whole 12 hours interval, and thus causes a strong decrease in the number of settled adults after 12 hours (Table 3).

The rate α_3 has been varied between 0.25 and 0.75 $\mathrm{min}–^{1}$. Although this has some effect on the rate at which leaving individuals start searching at short term (varying between 71.3 and 97.6% after 5 minutes), it hardly affects the behavioural dynamics or the number of settled adults during or after 12 hours (Table 3).

Fruit fly dispersal: D_H *and* ρ

The dispersal constant D_H (with standard value 0.058m^2 min^{-1}) of the fruit fly population has a strong effect on the behavioural dynamics of the settled fruit fly population. For increasing values of D_H between 0.029 and 0.087, the slope of the settled fruit flies graph increases, and hence the numbers of settled fruit flies present after 12 hours increases (Table 3). Thus, the farther the fruit flies can disperse the faster fruit flies find a resource and settle. Varying the velocity ρ of the ring-random dispersal from 0.5 to 1.5 m min^{-1} causes no noticeable effect on the behavioural dynamics (Table 3).

Table 3 Sensitivity analysis. The value in the third column is the reference value as used in the simulations. The fourth column contains alternative values for the parameters, all other parameters being on their reference values. The fifth and sixth column give the relative change in percentage of the number of fruit flies after a 12 hrs simulation $H_{\mathrm{tot},1}$ (12hr) and $H_{S,1}$(12hr). The seventh and eighth column give a qualitative comparison of the behavioral dynamics of the total and settled population numbers $H_{\mathrm{tot},1}(t)$ and $H_{S,1}(t)$, – – means much slower dynamics, – means slower dynamics, a blank means approximately equal dynamics, + means faster, + + much faster dynamics of the population.

Name	Description	reference value	alternative values	$H_{\mathrm{tot},1}(12)$	$H_{S,1}(12)$	$H_{\mathrm{tot},1}(t)$	$H_{S,1}(t)$
κ & η	attraction ratio	5.0 & 2.5	7.5 & 1.67 2.5 & 5.0	2.2 –2.2	3.6 –4.0		+ –
D_{H}	dispersivity of Drosophila	0.58	0.87 0.29	0.2 –3.5	1.3 –7.9	+ – –	+ – –
ρ	resource leaving flight speed	1	1.5 0.5	–0.4 0.3	–0.6 0.5		
α_1	settlement rate	0.25	0.375 0.125	1.9 –4.8	3.5 –9.5		 –
α_2	leaving rate	0.002	0.003 0.001	–5.1 6.9	–10.9 14.2	– +	– – + +
α_3	start-to-search rate	0.5	0.75 0.25	0.1 –0.6	0.2 –1.1		
D_{I} & μ	dispersivity & loss rate of chemicals	1.0 & 0.14	1.5 & 0.1 0.5 & 0.2	–1.5 5.9	–1.3 5.6	 +	 +
F_0	food odour saturation	10	15 5	3.7 –6.8	4.5 –8.2	 –	 –
A_0	pheromone saturation	0.04	0.06 0.02	2.9 –5.2	3.0 –5.5	 –	 –
θ_F	food odour production	2	3 1	–3.8 6.3	–4.6 7.5	– +	– +
θ_A	pheromone production	0.83	1.215 0.415	–2.8 4.9	–3.0 5.2	– +	– +
ω	pheromone evaporation	4.10^{-4}	6.10^{-4} 2.10^{-4}	–2.8 4.9	–3.0 5.2	– +	– +

Fruit fly response: F_0 and A_0

The half-saturation parameters F_0 and A_0 concerning fruit fly response toward food odours or aggregation pheromone, respectively, have a moderate effect on both the total and the settled population. Halving the values for F_0 or A_0, from 10 to 5 or from 0.04 to 0.02, respectively, slightly decreases the total number of fruit flies and the number of settled fruit flies after 12 hours (Table 3). Increasing the values for F_0 or A_0 by 50% did not have a great effect. Note that the effect of variation in F_0 is stronger than that in A_0. This is due to the fact that fruit flies only react to aggregation pheromone in the presence of food odours. It is reflected in the two terms in the sensory index, one depending on the food odour concentration, the other one depending on the product of food odour and pheromone concentration. Because of its structure, the latter term is equally sensitive to relative changes in food odour concentration and pheromone concentration. In combination with the first term, the sensitivity to relative changes in food odour concentration must be larger than the sensitivity to relative changes in pheromone concentration.

Attractiveness to infochemicals: κ *coupled with* η

As pointed out above, we couple κ (the ratio between random movement and odour-directed movement) and η (the parameter determining the relative attractiveness of pheromone in relation to food odour) in order to keep the 1:4.5 ratio of fruit fly numbers on substrates with food odour only (F) and food odour combined with aggregation pheromone (F+A) as observed by both Bartelt et al. (1985) and Wertheim et al. (2006). Therefore, in the sensitivity analysis we increase or decrease κ by 50%, and adapt η in such a way that the above mentioned 1:4.5 ratio is maintained. It is then found that the model was not sensitive to this parameter (Table 3).

3.4.2 Odour distribution: D_I coupled with μ

Decreasing the dispersal constant D_I of the infochemicals to values below 1 m_2 min^{-1} affects the behavioural dynamics of the total and the settled fruit fly population (Table 3). The total population size and the number of settled fruit flies in the first quadrant both increase faster for $D_I = 0.5$. Decreasing D_I thus increases the total number of fruit flies and number of settled fruit flies present after 12 hours. This indicates that fruit flies have less difficulty in finding the odour source when the dispersal of the infochemicals is slow. As the loss rate μ is fitted on the dispersal rate D_T and the time scale, its sensitivity was not analyzed separately. However, the reduction from 3D to 2D that is represented by this parameter may have a considerable effect on the model results.

3.4.3 Odour production parameters: θ_F, θ_A, and ω

Decreasing the production rate of food odours or aggregation pheromone (θ_F or θ_A respectively) had an effect on both the total and the settled population. When the production rate was halved, the total number of fruit flies and the number of settled fruit flies after 12 hours increased (Table 3). Doubling the value for θ_F or θ_A had no effect. Thus, more fruit flies could find the resources when there were less food odours or aggregation pheromone available in the air. This indicates that in our simulation both infochemicals where available in concentrations that caused saturation of the sensory system of the fruit flies. To understand this phenomenon, one should realize that in our model the fruit flies do not respond to the gradient of the infochemicals concentration itself, but to the gradient of the sensory index of the infochemicals. At full saturation, the sensory index has a constant level, and so its gradient vanishes. Then the fruit flies loose a directional cue, although the infochemical concentration may have a gradient that is quite useful at lower concentration levels. Thus, under conditions of saturation, fruit flies move at random, and have more difficulties in finding the resources.

The standard parameter values that we use are based on the experimental studies of Wertheim et al. (2006). We notice that in the setup in their study, the fruit flies are exposed to large amounts of food odour and pheromone. Therefore, it is not unreasonable that in these experiments the concentration level is close to saturation. From an evolutionary point of view, it seems plausible that the chemotactical abilities of fruit flies are better tuned to finding a resource when resources are scarce than in finding a resource quickly when resources are abundant.

The model was equally sensitive to variation in the evaporation rate of the aggregation pheromone, ω, as to the production rate θ_A (Table 3). Indeed, a clear interdependency of ω and θ_A can be observed. This is not surprising, as the amount of available pheromone odour that gets available per time unit depends on the product of ω and θ_A.

3.5. Conclusion and discussion

For a spatio-temporal model of *Drosophila* based on reaction to food odours and aggregation pheromone, realistic parameter values are hard to obtain. In general, any model for the reaction of insects on odour in the air can be divided into three parts:

1. A model for insect behaviour where the population members are divided among states depending on their activity.
2. A model for production, evaporation and dispersion of the odour substances.
3. A model for the detection of odours by insects, and their reaction thereupon.

The further investigation and parameterization of these submodels requires input from quite different disciplines. The first submodel lies in the field of behavioural ecology. As mentioned, the transitions between the three states are known from a biological point of view, because the *Drosophila*-based food web is already thoroughly studied (e.g., Wertheim, 2001). Quantitative measures of the rate α_1 at which the searching flies C in the close vicinity of a resource item settle, the rate α_2 at which the settled flies S leave their resource, and the rate α_3 at which leaving flies L start searching again still lack. As these parameters model population processes that have their roots in individual insect behaviour, more accurate estimates should be obtainable from insect behavioural experiments, either in artificial setups, or in the field, or both. A study by Wertheim et al. (2002) indicates that fruit flies after an initial choice for a resource mostly stay on that substrate for (at least) 2 hours. Therefore, the choice of 0.02 for the patch leaving rate $\alpha 2$ seems reasonable. Still, research on the patch residence time of *D. melanogaster* that can be translated to the population level responses is needed. The same applies to oviposition rates of *Drosophila*.

The second submodel lies in the field of physics, organic chemistry, and micrometeorology. A good measurement of evaporation rates seems to be within reach; also a possible degradation of infochemicals can be studied. Models for plume transport on short and intermediate distances should be investigated further. As we have shown, the reduction of the three-dimensional dispersion of infochemicals to two dimensions may lead to concentration patterns that are qualitatively and quantitatively different. These differences can be remediated only in part with the parameterization. Therefore, it may be interesting to investigate to what extent the results from a full 3D spatial model for insect behaviour agree with the results that we find with our essentially 2D model.

The third submodel lies in the field of biophysics and neurology. This submodel may be the most challenging. Although some knowledge exists on how fruit flies react to aggregation pheromone (Wertheim et al., 2002a), nothing is known about the spatial dose-response relationship to food odours and aggregation pheromone. In the model for the reaction of fruit flies to infochemicals that we used, two parts may be distinguished: the sensory index function that describes the perception of our virtual fruit flies to infochemicals, and an additional parameter ν describing the strength of chemotaxis as compared to random walk movement. At this moment, quantitative data are so scarce that this submodel is clearly overparameterized. We have solved this problem by fixing a combination of the parameters κ and η. It will not be easy to decouple these parameters just by ethological experiments, as this would require a very controlled setup to establish a quantitative relation between fruit fly behaviour and measured infochemical concentration gradients. More fundamentally, one may discuss the type of the sensory index function that we used. For a sensory index function for one infochemical, the use of a Michaels–Menten type of function for saturated response can be made plausible from the limited availability of sensory nerve cells to accommodate infochemical molecules (e.g., Postma, 2003). However, for two interrelating infochemicals, many types of sensory index functions are conceivable, and we have chosen a simple one from them. It may require neurological research on fruit flies to validate this choice.

The sensitivity analysis shows that the model is most sensitive to changes in the fruit fly dispersivity D_H and the patch leaving rate α_2. It should be feasible to obtain better information on these parameters in controlled experiments, either in the field or in the laboratory. A second group of sensitive parameters are the infochemical parameters ω, θ_A and θ_F , especially at the lower density levels. This sensitivity might be caused by the sensory response function that we have adopted. However, independent of the sensory response function, this sensitivity highlights the importance of a careful treatment of the infochemical loss. Insight into the spatial ecology of aggregation should be derived from a multidisciplinary approach that includes the identification of the cues that mediate aggregation, the behavioural responses of individuals to these cues, and the spatial variation in the responses that result from spatial variation in pheromone distribution. With the results of the sensitivity analysis in mind, especially reliable estimates for the parameters A_0, F_0, D_I , D_H , and $\alpha 2$ are required. This is exactly what we plan to obtain in future experiments. However, even without these experiments, the sensitivity analysis shows that the overall conclusions in **Chapter 2** for the resource density of 5 apples per m2 hold over a wide range of plausible parameter values. The same probably applies for other resource densities.

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Picture Marjolein Lof

Chapter 4

Odour mediated aggregation enhances the colonization ability of *Drosophila melanogaster*

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Abstract

Animal aggregation is a general phenomenon in ecological systems. Aggregations are generally considered as an evolutionary advantageous state in which members derive the benefits of mate choice and protection against natural enemies, balanced by the costs of limiting resources and intraspecific competition. Many insects use chemical information to find conspecifics and to form aggregations. In this study, we describe a spatio-temporal simulation model designed to explore and quantify the effects of the strength of chemical attraction, on the colonization ability of a fruit fly (*Drosophila melanogaster*) population. We found that the use of infochemicals is crucial for colonizing an area. Fruit flies subject to an Allee effect that are unable to respond to chemical information could not successfully colonize the area and went extinct within 4 generations. This was mainly caused by very high mortality due to the Allee effect. Even when the Allee effect did not play a role, the random dispersing population had more difficulties in colonizing the area and is doomed to extinction in the long run. When fruit flies had the ability to respond to chemical information they succesfully colonized the orchard. This happened faster, for stronger attraction to chemical information. In addition, more fruit flies were able to find the resources and the settlement on the resources was much higher. This resulted in a reduced mortality due to the Allee effect for fruit flies able to respond to chemical information. Odour mediated aggregation thus enhances the colonization ability of *Drosophila melanogaster*. Even a weak attraction to chemical information paved the way to successfully colonize the orchard.

Keywords Chemotaxis · Aggregation · Integro-Difference equations · Spatial population dynamics · Allee effect

4.1. Introduction

Aggregation is a general phenomenon in the animal kingdom (Parrish and Edelstein-Keshet, 1999). It can especially be beneficial when a population is small and has to overcome negative effects associated with low population densities. Such negative effects, known as the Allee effect (Allee, 1931), or a reduced per capita growth rate at low population densities, can for instance occur due to difficulties in finding a mate or difficulties in resource exploitation (Wertheim et al., 2005). Protection from predators is viewed as an important selective advantage to group membership resulting from aggregation (Parrish and Edelstein-Keshet, 1999, Wertheim et al., 2005). Protection from environmental conditions can also be a benefit from aggregation (see for instance Gilbert et al., 2006). Furthermore, in temporary habitats (e.g. habitats in early stages of ecological succession, ephemeral ponds, annual plants or fermenting fruits) aggregation is generally considered to promote coexistence of species competing for resources, by reducing the impact of interspecific competition relative to that of intraspecific competition (Atkinson and Shorrocks, 1981, Shorrocks and Sevenster, 1995, Krijger and Sevenster, 2001). However, aggregation also involves costs, individuals within an aggregation frequently experience more severe competition for food, space and mates than when they would be on their own. Moreover, within a group a pathogen can be more easily transmitted, than between solitary individuals. Also the group as a whole can be more conspicuous to natural enemies (Parrish and Edelstein-Keshet, 1999).

In *Drosophila melanogaster* adult aggregation has a positive effect on larval survival because adults alter the suitability of the resource for the juveniles: the presence of adults prior to larval development increases the amount of food that is present for the larvae. Adults, especially females, vector a diversity of yeasts and inoculate the resource with these yeasts during their presence (Morais et al., 1995). At the same time, this increase in yeast also reduces fungal growth (Wertheim et al., 2002). This positively affects larval survival, because strong fungal growth can cause a high mortality in fruit fly larvae (Rohlfs et al., 2005, Rohlfs, 2006). Furthermore the larva of *D. melanogaster* themselves are also able to suppress fungal growth by disrupting the hyphae of the fungus. Larger groups of larva are more successful at this than smaller groups or single larvae (Rohlfs et al., 2005, Rohlfs, 2008). The local interaction with the fungi gives rise to an Allee effect in larval development. However, aggregation formation can also have negative effects. Rohlfs and Hoffmeister (2003) show that the survival from egg to adulthood for *Drosophila subobscura* is hump shaped, with low survival not only at low population numbers but also at high population numbers. This indicates the presence of a cost to aggregation. At high local population densities larval survival decreases due to competition (Wertheim et al., 2002, Hoffmeister and Rohlfs, 2001).

In this study we do not have an Allee effect in its classical definition – i.e. we do not look at the per capita growth rate of the total population (Stephens et al., 1999, Taylor and Hastings, 2005, Berec et al., 2007). Instead we study the local larval survival (as in Etienne et al., 2002, Wertheim et al., 2002, Rohlfs, 2008). This local larval survival is positively density dependent, i.e. is reduced at small local larval population size due to competition with fungi. This, in combination with the negative density dependence due to intraspecific competition, can possibly give rise to a demographic Allee effect (Stephens et al., 1999). In this study we define the Allee effect as the negative effect of small local larval population size on local larval survival.

The fruit fly *D. melanogaster* breeds in ephemeral substrates, e.g. fermenting fruit. In their natural environment these substrates are distributed unevenly. Fermentation products, produced by micro-organisms that live on food sources, and aggregation pheromone, emitted by recently mated females, play through chemical attraction a directive role in the localization of and aggregation on these substrates (Hutner et al., 1937; West, 1961; Bartelt et al., 1985; Wertheim et al., 2006).

In a previous model study we showed that the use of infochemicals, such as food odor and the aggregation pheromone, was mainly beneficial during spatial expansion and at small population sizes (Lof et al., 2008; **Chapter 2**). Under such circumstances the positive effects of reduced mortality at the newly colonized resources outweigh the costs of increased competition in already colonized parts of the domain. However, when the whole orchard was colonized and the population is large, the negative effects of increased mortality due to competition are higher when fruit flies can use chemical information, resulting in a negative effect of the infochemicals on the population numbers as compared to the situation with random dispersal. In that previous model study, fruit flies were introduced in the centre of the orchard. In this set-up the chance of finding a resource was very high, even for the random dispersing fruit fly population. In reality, adult *D. melanogaster* hibernate in human shelters (Boulétreau-Merle et al., 2003). Therefore, the fruit fly population has to re-colonize the orchard each year after winter. In this situation, the chance of finding a resource by random dispersal is much lower. We argue that in this situation guidance of the fruit flies by chemical information plays a more profound role in locating the resources.

In the present study the focus is on the role of different strengths of chemical attraction on the ability of the fruit fly population to colonize an area from outside the boundaries, both with and without an Allee effect as described above. Therefore, we use a spatio-temporal model that incorporates odours distribution and population responses (as in Lof et al., 2008; **Chapter 2**). To investigate the costs and benefits of the use of infochemicals, we compare larval mortality due to the Allee effect or competition and its net effect on population numbers for different strengths of chemotactical attraction. As a reference we also compare the found results with the situation where fruit flies are unable to respond to chemical information. To study the impact of the Allee effect on population dynamics, we also look at the situation without an Allee effect, but with competition at high larval densities.

4.2. Description of the model

4.2.1 Population dynamics and dispersal of fruit flies

Within-generation dynamics

In our model, we consider female fruit flies only. This female fruit fly population is divided according to three activities they can exhibit. The searching subpopulation (with density H_C) uses chemical information to find a suitable resource, a yeast infected apple. Once they found a resource, they settle down with a rate α_1 (min^{-1}). They become part of settled subpopulation (with density H_S), whose members forage and mate on the resource. Members of the settled subpopulation have a leaving rate from the resource of α_2 (min^{-1}). In doing so they join the leaving subpopulation (with density H_L), which actively move away from the resource. A member of the leaving population starts to search for a new resource with rate α_3 (min^{-1}) and becomes a member the searching subpopulation. The equations relating these state variables are

$$R(x,y) = \begin{cases} 0 & \text{if no apples are present at position } (x,y) \text{ at time } t \\ 1 & \text{if an apple is present at position } (x,y) \text{ at time } t \end{cases} \tag{1}$$

$$\frac{\partial}{\partial t} H_C = \alpha_3 H_L - \alpha_1 R H_C \tag{2}$$

$$\frac{\partial}{\partial t} H_S = \alpha_1 R H_C - \alpha_2 H_S \tag{3}$$

$$\frac{\partial}{\partial t} H_L = \alpha_2 H_S - \alpha_3 H_L \tag{4}$$

In equations 2-4 we did not mention the time and spatial coordinates explicitly, but all dynamic variables depend on time and position. Within a generation, the total number of adult fruit flies is kept constant on an extended grid with the orchard in the center. However, the distribution over the three activity states does change over time. Members of the searching and the moving subpopulations are able to leave the orchard with the resources, and, as they start outside the orchard, there is even a possibility that they never enter it. We assume that during the three dispersal days there is no adult mortality.

Fruit fly dispersal

The searching subpopulation (H_C) uses chemical information to find a resource. We assume that they can respond to the gradient of infochemicals and use chemotaxis to find a resource (Eq. 5) (Keller and Segel, 1971). The strength of the attraction is determined by the chemotaxis coefficient ν. When chemical information is absent, the searching population can only disperse randomly, with dispersal coefficient D_H. The fruit fly response to food odours (with density F) and the aggregation pheromone (with density A) is modelled as a Monod function (Monod, 1949). Bartelt et al (1985) showed that fruit flies respond to the combination of food odours and the aggregation pheromone and are also attracted to food odours alone. They however, do not respond to the aggregation pheromone without food odours also present. Equation 6 gives a description of the response of *D. melanogaster* to food odours and the aggregation pheromone

$$\frac{\partial}{\partial t} H_C = D_H \nabla^2 H_C - \nabla \cdot \left[\nu H_C \nabla f(F, A) \right] \tag{5}$$

$$f(F, A) = \frac{F}{F_0 + F} + \eta \frac{FA}{F_0 A_0 + FA} \tag{6}$$

where F_0 and A_0 are the concentrations of food odours and the aggregation pheromone, respectively, at which the response is half the maximum and η is a measure for the relative strength of the response on the combination of food odours and the aggregation pheromone as compared to the response to only food odours.

While the movement of searching fruit flies is directed by chemical information, the movement away from the resource by the moving fruit fly population is not affected by the presence of food odours and the aggregation pheromone. The fruit flies come into the moving state by actively flying away from their resources. We assume that the fruit flies actively fly away with a velocity ρ from the resource in an arbitrary direction and afterwards disperse randomly. This process cannot be modelled with ordinary or partial differential equations; in an integro-difference equation it is modelled with a ring random dispersal kernel (Lof et al., 2008, **Chapter 2**). We chose this type of dispersal to ensure that the majority of the moving population actually leaves the resource. If the population were to start searching for a resource immediately by using chemical information, the majority of the fruit flies would return to the same resource.

Between-generation dynamics: reproduction

Per generation, lasting 21 days in reality, we simulated three dispersal days, during which fruit flies are actively dispersing and reproducing. Adult females that have settled on a resource deposit ξ eggs per minute on average. The cumulative number of eggs on a resource after the 3 days (in generation n (Eq. 7)) determines whether larvae develop successfully into adult fruit flies in the next discrete generation. The larvae develop into adults in 18 days. We do not model the development explicitly, but we only calculate what fraction of the larvae survive and constitute the next generation. The fraction of the larvae that survive on one resource are highest for intermediate numbers of larvae (Eq. 8). When only a small number of larvae is present on an apple, a fraction dies due to the Allee effect, while mortality due to competition plays a role when many larvae are present. Of the surviving larvae, a fraction φ is female. At the end of a generation the total adult population dies and half of the surviving larvae constitute the next adult female generation. Furthermore, we assume that at the end of a generation all resources are either depleted or unsuitable for reproduction. Therefore, there is no resource anymore at the beginning of the next generation when the new adults emerge from the pupae. The new generation of adult fruit flies has to start searching for a new resource immediately. In our simulation these resources are randomly placed at the beginning of each generation.

$$N(x,y,n) = \int_0^3 \xi H_S(x,y,n)\, dt\,. \tag{7}$$

$$\begin{aligned} H_C(x,y,n+1) &= \varphi\, N(x,y,n)\, s_A(N)\, s_C(N)\,, \\ s_A(N) &= \frac{1}{1+e^{-c_A(N-N_A)}}\,, \quad s_C(N) = \frac{1}{1+e^{c_C(N-N_C)}} \end{aligned} \tag{8}$$

4.2.2 Odour distribution

D. melanogaster responds to food odours (F) and its aggregation pheromone (A). Aggregation pheromone is not excreted as a volatile, but as a fluid accompanying the eggs. We therefore divide the aggregation pheromone in two phases: a liquid or adsorbed form (with density A_R) at the resource, that slowly evaporates into a gaseous form (A) that searching fruit flies can detect in the air. We assume that no wind is present and that these odours thus diffuse randomly, i.e. going in any direction with an equal probability. Turbulent odour diffusion is a much faster process than the dispersal of adult fruit flies. Because odour diffusion is a 3-dimensional process, while we model in two dimensions, we introduced a loss term (μ) to represent odour molecules that gets out of reach of the searching population through diffusion in a vertical direction.

$$\frac{\partial}{\partial t}F = D_I \nabla^2 F - \mu F + \theta_F R \tag{9}$$

$$\frac{\partial}{\partial t}A = D_I \nabla^2 A - \mu A + \omega A_R \tag{10}$$

$$\frac{\partial}{\partial t}A_R = \theta_A H_S - \omega A_R \tag{11}$$

The description and value of all the parameters in the model are given in Table 1. For more details on how these values are arrived at, we refer to **Chapter 3**.

Table 1 The model parameters involved in the short time dynamics and their values.

Name	Description	Value	Units
Δt	Time step short term population dynamics	5	min
Δx, Δy	Spatial step size	0.1758	meter
D_H	Dispersion coefficient of at random moving fruit flies	0.058	$m^2\ min^{-1}$
α_1	Settlement rate of searching fruit flies	0.25	min^{-1}
α_2	Rate of settled fruit flies leaving the resource	0.002	min^{-1}
α_3	Rate of leaving fruit flies that start searching for resources	0.5	min^{-1}
ρ	Velocity of movement away from the resource	1	$m\ min^{-1}$
F_0	Saturation parameter for food odours	10	$ng\ m^{-2}$
A_0	Saturation parameter for the aggregation pheromone	0.04	$ng\ m^{-2}$
D_I	Dispersion rate of infochemicals	1	$m^2\ min^{-1}$
μ	Loss rate of infochemicals	0.025	min^{-1}
θ_F	Food odor production by the resource	2	$ng\ apple^{-1}\ min^{-1}$
θ_A	Aggregation pheromone production by settled fruit flies	0.83	$ng\ fly^{-1}\ min^{-1}$
ω	Evaporation rate of liquid aggregation pheromone	4.10^{-4}	min^{-1}
v	Attraction towards infochemicals	$5D_P$	-
κ	Relative strength of movement towards infochemicals compared to random dispersal	5	-
η	Attraction ratio of food odour together with aggregation pheromones relative to the attraction to food odour alone	2.51	-
ξ	Fecundity of the settled population	0.0083	min^{-1}
φ	Sex ratio of the larvae (fraction of females)	0.5	-
N_A	Number of larvae per apple at which 50 % survives the Allee effect	25	-
N_C	Number of larvae per apple at which 50% survives competition	250	-
c_A	Slope sigmoid survival curve modelling the Allee effect	0.088	-
c_C	Slope sigmoid survival curve modelling the competition	0.044	-

For dimensionless parameters the '-' sign is used.

4.2.3 Numerical approach

In the numerical solution of the model equations, the odour and fruit fly dispersal was treated separately from the adult fruit fly population dynamics. Odour distribution, odour evaporation and dispersal by the moving and searching fruit fly population were solved using the integro-difference approach (as in Neubert et al., 1995, Powell et al, 1998). In this approach, dispersion is treated as a process separately occurring in time. The analytical solution of this process is used in the simulation model. This is an effective approach, because it allows us to take large time steps, without running into any numerical stability problems.

Odour distribution and odour evaporation

The distribution of odours is calculated by taking the convolution product of the odour density and the probability density function, or dispersal kernel (denoted by *K*), for random diffusion, described by

$$K(x, y, \Delta t) = \frac{1}{4\pi D_I \Delta t} e^{-\frac{x^2 + y^2}{4D_I \Delta t}} \tag{12}$$

where Δt is the time step taken and D_I is the diffusion constant of the infochemicals.

During each time step, food odours and the aggregation pheromone evaporate into the air. The dispersal of the produced odour is calculated by taking the convolution product of the odour produced per minute and a dispersal probability function for a continuously producing source. The distribution of the produced odour is described by

$$K(x, y, \Delta t) = \int_0^{\Delta t} \frac{1}{4\pi D_I t} e^{-\frac{x^2+y^2}{4D_I t}} dt = \frac{1}{4\pi D_I} Ei\left(\frac{x^2 + y^2}{4D_I \Delta t}\right) \tag{13}$$

where *Ei* is the exponential integral.

Ring random dispersal

Ring random dispersal, used to model the movement away from the resource of the moving population, is described by

$$K(x, y, \Delta t) = \frac{1}{4\pi D_H \Delta t} e^{-\frac{(\sqrt{x^2 + y^2} - \rho \Delta t)^2}{4D_H \Delta t}} \tag{14}$$

where ρ is the velocity of the displacement away from the resource and D_H is the diffusion constant of the fruit fly population.

Dispersion of the searching population

The movement of the searching population (H_C) is directed towards the odour source by the concentration gradient of the infochemicals. The change in the spatial distribution of searching fruit flies (Eq 5.) can be approximated by first making a change of variables as in Powell et al. (1998)

$$\frac{\partial}{\partial t} \tilde{H}_C = D_H \nabla^2 \tilde{H}_C + v \nabla f(F, A) \cdot \nabla \tilde{H}_C \tag{15}$$

where,

$$H_C = \tilde{H}_C \cdot \exp\left(-\tfrac{v}{D_H} f(F, A)\right) \tag{16}$$

with,

$$\tilde{H}_C(x, y, 0) = \exp\left[-\frac{v}{D_H} f(F, A)\right] H_C(x, y, 0) \tag{17}$$

and advancing H_C using a truncated asymptotic series approximation for $\widetilde{H}_C$,

$$\widetilde{H}_C(t) \approx \sum_0^i v^i \widetilde{H}_i(x,y,t) \tag{18}$$

with,

$$\widetilde{H}_0(x,y,T) = K(x,y,T) * \widetilde{H}_0(x,y,0)$$
$$\widetilde{H}_i(x,y,T) = \int_0^T K(x,y,T-t) * \left[\nabla f \cdot \nabla \widetilde{H}_{i-1}(t)\right], \qquad for\ i \geq 1,\ \widetilde{H}_i(x,y,0) = 0$$

and a numerical approximation (Simpson's rule) for the integral.

4.3. Simulation set-up

We considered a spatial domain of 90 m × 90 m, with the orchard in the centre. It is divided into 512×512 cells with a diameter of 0.1758 m[*]. The simulations were carried out with an IDE method that intrinsically uses periodic boundary conditions. To eliminate the unwanted effects of these boundary conditions, the 90 m × 90 m domain was embedded in the centre of an enlarged domain of 180 m × 180 m. On this large domain, the actual simulations were done. This setup is the best approximation of a real world situation, where the domain containing the orchard is neither surrounded by a wall of doom, nor by a reflecting wall, nor by periodic boundary conditions; instead, there is an unspecified surrounding, into which the flies may enter and from which they may return, driven by random dispersion and chemotaxis. Of course, this surrounding area has an outer boundary again, but this is so far from the actual domain of interest that its influence there is negligible.

We ran simulations for one breeding season, consisting of ten discrete generations. Per generation, we simulated three dispersal days, each consisting of twelve hours, divided in 144 time steps of 5 minutes, during which the fruit flies are actively dispersing or reproducing. At the end of a generation, we calculate larval mortality due to the Allee effect and due to competition. The female adults, i.e. half of the surviving larvae, constitute the next adult population.

The attraction ratio $\kappa = v/D_H$ is a measure of the relative strength of the attraction towards infochemicals as compared to the random dispersion constant of the fruit flies. We studied the role of attraction to chemical information on the ability to find the resources, measured by the settlement on the resources, by comparing the fruit fly behaviour at four levels of κ namely: no attraction, that is, random dispersal only (κ=0), weak attraction (κ=1), intermediate attraction (κ=5) and strong attraction (κ=10).

We ran the simulation for a resource density of 0.1 apples m^{-2}, representing an orchard where resources are scarce. The resources were randomly distributed in the centre of the domain (60 m × 60 m). To mimic the natural situation, for each generation of flies, the apples were randomly placed. In the initial set-up, we established a 5 meter-wide buffer zone without apples or adult fruit flies around the area containing apples.

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[*] We used the factor 512 because it enhances the efficiency of the numerical computations of the integro-difference approach, as powers of 2 allow use of the fast Fourier transform for the convolutions. It does not influence the results essentially.

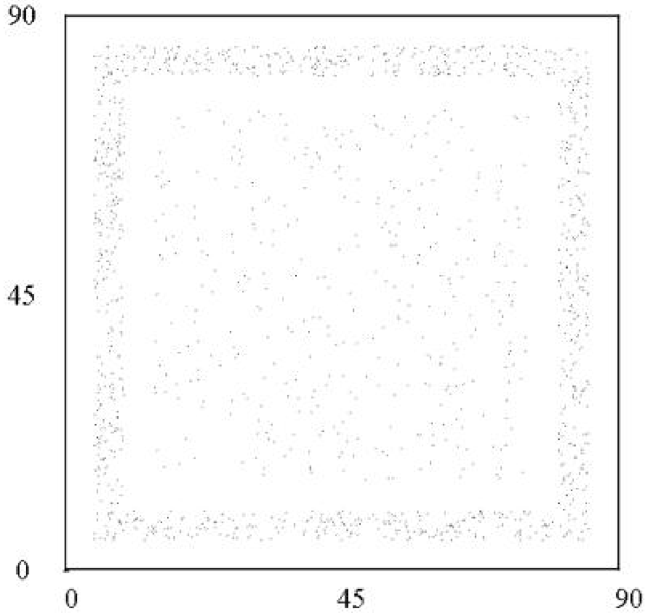

Figure 1 Spatial set-up of the domain (90 m × 90 m). The resources are randomly distributed in the centre of the domain (60 m × 60 m) and a zone (5 meter wide and 5 meters apart from the orchard) with randomly distributed adult fruit flies around it. The white areas contain no apples or fruit flies.

At the beginning of the simulation we released 1000 adult fruit flies, randomly distributed in a 5 meter-wide zone around the buffer zone outside the orchard (Fig. 1). We ran the simulation 3 times to verify the consistency of the results.

Statistics
To test the effects of infochemical use on settlement and on larval survival we used the G-independence test on the average number of settled and dispersing fruit flies in the first generation in the orchard for the different levels of attraction towards infochemicals. For the larval survival in the first generation we used the test on the number of larvae that survived or died for the different levels of attraction towards infochemicals (Sokal and Rohlf, 1981).

We used linear mixed models to test the effect of the use of infochemicals on the mortality due to the Allee effect (%), mortality due to competition (%). We used an arcsine square root transformation for the mortality due to the Allee effect and a logarithmic transformation for the mortality due to competition, because the values in the latter differed in several orders of magnitude; ranging between 0.002% and 67%. For the first three generations we compare all four levels of attraction (“treatments”), because in these generations the fruit flies that could not respond to chemical information were still present. In all 10 generations we only could compare the three situations where fruit flies were able to respond to chemical information (κ=1, κ=5 and κ=10). To test the effect of chemical use on the ability to find the orchard in the first generation, we compared the total number of fruit flies in the orchard for each attraction level during the first three days with a 3-hour time-step.

The linear mixed effect model is especially suitable for data where the measurements are correlated in time. In the model we took “generation” as repeated measurement, and “treatment”, “generation” and “treatment x generation” as fixed effects. We tested the model for four different covariance structures, compound symmetry (CS), first-order autoregressive (AR(1)), heterogeneous first-order autoregressive (ARH(1)) and an unstructured covariance matrix (UN). The heterogeneous first-order autoregressive was the best model for the data (it had the lowest AIC). For these statistics we used SAS 9.1.

4.4. Results

The presence of chemical information had a positive effect on the ability of fruit flies to colonize an orchard (Fig. 2). The stronger they responded to chemical information, the faster the population was able to find the orchard (Fig. 2). The total population in the orchard for each time step was significantly higher for increasing attraction to infochemicals (**P**<0.0001 for all combinations of treatments). Furthermore, the population growth was faster for stronger attraction to infochemicals (Fig. 3a).

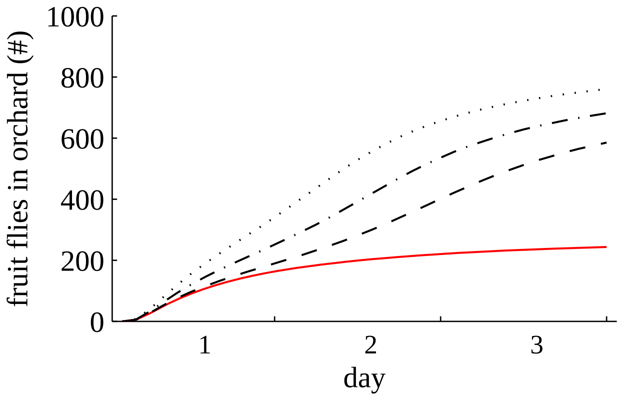

Figure 2 The dynamics of the total fruit fly population in the orchard (60x60m) in the first generation, consisting of 3 dispersal days, when fruit flies could not use chemical information ($\kappa = 0$, solid red line), when the attraction to infochemicals was weak ($\kappa = 1$, dashed line), intermediate ($\kappa = 5$, dash dotted line), or high ($\kappa = 10$, dotted line).

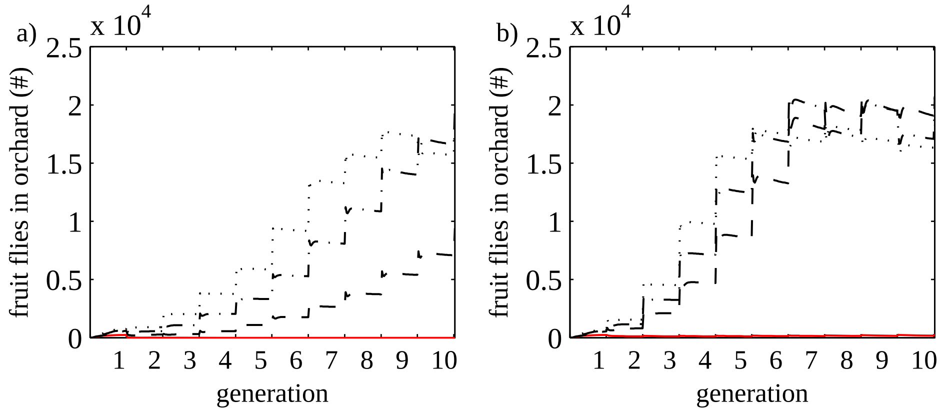

Figure 3 The dynamics of the total fruit fly population in the orchard (60x60m) for all 10 generations a) with an Allee effect, b) without an Allee effect, when fruit flies could not use chemical information ($\kappa = 0$, solid red line), when the attraction to infochemicals was weak ($\kappa = 1$, dashed line), intermediate ($\kappa = 5$, dash dotted line), or high ($\kappa = 10$, dotted line).

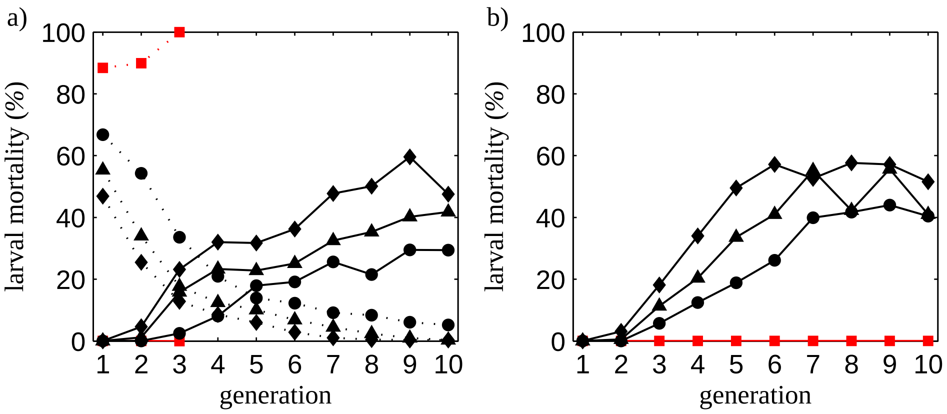

Figure 4 Larval mortality due to the Allee effect (dotted lines) and competition (solid lines) for each generation a) with an Allee effect, b) without an Allee effect, for the control simulation where fruit flies could not respond to chemical information (κ =0, red square) and for the simulations with weak (circle), intermediate (triangle) and strong (diamond) attraction to infochemicals (κ = 1, 5 and 10, respectively). Note that in 4a) the larval mortality for κ = 0 is given for the first three generations only, because the population got extinct after the third generation

When fruit flies could not respond to chemical information, and thus only dispersed randomly, the population was not able to colonize the orchard. The population went extinct within 4 generations, – population numbers of less than 1 fruit fly in all three runs (combined Fig 2 and 3a). This was mainly caused by a high larval mortality due to the Allee effect: around 90% per generation until the population became extinct (Fig. 4a). The number of fruit flies that found the orchard, as well as, the number of fruit flies within the orchard that found a resource and settled down, differed between the situations where fruit flies had the ability to use chemical information or not; the settlement when fruit flies could respond to chemical information was around 40-45%, while the settlement when they could not respond to chemical information (κ=0) was significantly lower (G=10.650, G=16.527 and G=22.422, **P**<<0.001 for κ=1, 5 and 10 respectively), around15-20 % (Fig. 5). This indicates that the use of chemical information induces aggregation on the resources.

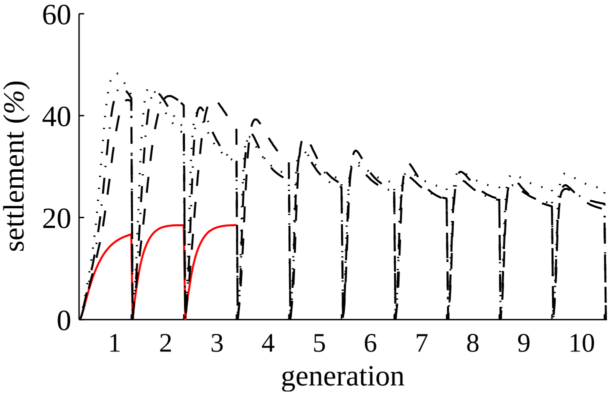

Figure 5 The dynamics of the settlement (%) of fruit fly population in the orchard (60x60m) for all 10 generations for the simulations including an Allee effect, when fruit flies could not use chemical information (κ = 0, solid red line), when the attraction to infochemicals was weak (κ = 1, dashed line), intermediate (κ = 5, dash dotted line), or high (κ = 10, dotted line). Note that the percentage of settlement for κ = 0 is given for the first three generations only, because the population got extinct after the third generation.

When fruit flies could respond to chemical information, the mortality due to the Allee effect in the first generation was significantly lower than when they dispersed randomly (κ=0): between 50 and 70 % for a weak respectively strong attraction towards infochemicals (Fig. 4) (G=22.261, G=47.448 and G=73.731, **P**<<0.001 for κ=1, 5 and 10 respectively). The mortality due to the Allee effect in the first generation was significantly lower for stronger attraction to infochemicals; the mortality for κ=5 and κ=10 (G=14.335, G=47.464, both **P**<<0.001) were significantly lower than for κ=1, and the mortality for κ=10 was also significantly lower than for κ=5 (G=10.708, **P**<0.0025). Moreover, there was a significant trend in time, i.e. the mortality due to the Allee effect decreased significantly and mortality due to competition increased significantly (both **P**<<0.001). The mortality due to the Allee effect decreased more rapidly for stronger attraction to chemical information (the decrease for κ=5 and κ=10 was stronger than for κ=0 and κ=1 **P**<<0.001, and the latter was stronger than for κ=0, **P**<<0.001). The reduction in the mortality due to the Allee effect is caused by aggregation on the available resources in response to infochemicals. However, this aggregation also caused an increase in mortality due to competition. Still, the presence of chemical information had a net positive effect on population numbers (Fig. 3a).

In our simulations where we assume that the Allee effect does not have an effect on larval survival, we also found that the ability respond to chemical information positively affected the population growth of the fruit flies in the orchard. Without an Allee effect the population growth was faster (Fig 3b) and the mortality due to competition increased more rapidly (Fig 4b). When fruit flies could use chemical information the population growth levelled off in the seventh generation, because the population reached its carrying capacity set by competition. If however, the Allee effect played a role, the fruit fly population just reached its carrying capacity in the tenth generation, and only for the fruit fly populations that were strongly attracted to chemical information (Fig 3a). As expected, even when the Allee effect is absent, fruit flies unable to use chemical information still have more difficulties in colonizing the orchard. After the first generation they decrease in number. From the second generation on there is a very slow population growth (from 190 to 245 fruit flies), and they are able to persist 10 generations. It should be noted that after 10 generations the total number of fruit flies is only one fourth of the initial population size. If we would simulate multiple breeding seasons, the population would not be able to persist. To check whether this slow growth was due to the fact that we started with a too small number of fruit flies, or just due to the fact that they could only disperse randomly, we simulated random dispersal with an initial population of 2000 and 2500 fruit flies. These simulations showed the same results of initial decrease after the first generation and then slow growth. This indicates that the slow growth was mainly because they had more difficulties in finding a resource. As in the simulations including an Allee effect, the settlement of the random dispersing population was only around 15-20% each generation. Due to this lower settlement, fewer eggs are laid and thus the population growth is less strong. What also plays a role for the reproduction is that a larger part of the fruit flies left the orchard. At the end of a generation only 70% was still in the orchard, while when they were able to respond to chemical information 95-98% remained in the orchard.

Summarising, the simulations show that the use of chemical information is crucial for colonizing an area when an Allee effect plays a role, as a random dispersing population was not able to overcome the Allee effect associated with small population sizes. However also without an Allee effect, the random dispersing population had a much lower population growth, and at the end of generation 10 the total number of fruit flies was much lower than the initial population. Indicating that the population is unable to persist multiple breeding seasons, when fruit flies have to colonize the area at the beginning of each breeding season. The use of chemical information is not without costs; at large population sizes aggregation causes competition at the resources and thus increased mortality due to competition.

4.5. Conclusions and discussion

We found that the presence of chemical information is essential for population persistence when resources are scarce. During colonization of an area, populations that cannot use chemical information suffer from extremely high larval mortality (>90%) due to the Allee effect. This was mainly because these populations had more difficulties in locating a resource and were not able to aggregate on suitable resources. Even when the Allee effect did not play a role, the random dispersing population had more difficulties in colonizing the area. Difficulties in locating the resources caused that the population could only grow very slowly. At the end of the breeding season the population size was only one fourth of the initial adult population, indicating that the population is doomed to extinction in the long run. When the fruit flies had the ability to respond to chemical information, the settlement (%) on the resources was much higher, because more fruit flies were able to find the resources, and consequently the mortality due to the Allee effect was much lower. This increased settlement indicates that the response to chemical information causes aggregation on the available resources. However, the use of chemical information is costly - aggregation on the resources also causes an increase in mortality due to competition. Still, there is an overall net positive effect of the use of chemical information on population numbers during population growth. The mortality due to competition can be quite severe especially when the attraction towards chemical information is high: 40 to 60% larval mortality. High mortality due to competition does, however, not have the same dramatic effect on population size as mortality due to the Allee effect. For mortality between 50 and 55%, the population size remains constant. If mortality is higher than 55 % the population decreases and if it is lower than 50% the population increases. Nonetheless, if we were to look at individual level the costs of using chemical information could be severe.

It seems contradictory that fruit flies use chemical information when there are clearly costs involved. Yet, if we take into account that our simulated fruit fly population subject to an Allee effect could not use chemical information was unable to colonize the orchard and became extinct within 4 generations and without the Allee effect the population was reduced to one fourth of the initial population at the end of the breeding season, the ability to use chemical information is beneficial when an area has to be re-colonized each breeding season. This is the case for *D. melanogaster*, who cannot survive the winter in the field in the Netherlands. Adult *D. melanogaster* hibernate in human shelters and re-colonize the orchards from the boundaries in spring (Boulétreau-Merle et al., 2003). We showed that, in this case, using chemical information is essential for the ability of the population to colonize the orchard successfully. In the Netherlands most orchards only have one specific fruit species (monocultures) and each fruit species is only present for a short time. Under these conditions fruit flies have to switch between resource types, therefore the ability to colonize a new area is even more important.

This study partly explains why fruit flies use chemical information in spite of the costs of increased mortality. Chemical information is not only used by fruit flies, but can also be misused by a natural enemy that uses it to find its host (Dicke et al., 1994). The most important natural enemies of *Drosophila* are larval parasitoids (Janssen et al., 1988).

Wertheim et al. (2006) found that in the field 67% of apples contained larva of a Drosophila species that were parasitized by the larval parasitoids of the genus *Leptopilina*. We plan to investigate the role of chemical information in spatial host-parasitoid interaction. It has been postulated, in the “selfish herd” theory, that individuals in an aggregation experience a diluted risk of attack from natural enemies (Parrish and Edelstein-Keshet, 1999; Wertheim et al., 2005). If this is true, attraction towards chemical information has a positive effect on population numbers by decreasing the risk of parasitism. Rohlfs and Hoffmeister (2004) did indeed find that the risk of parasitism could decrease for higher numbers of larva of *Drosophila subobscura* in apples and plums. This was mainly because at higher larval densities the larvae could move deeper into the resource, which provides a spatial refuge against larval parasitoids. On the other hand, Wertheim et al. (2003) found that the aggregation pheromone used by *D. melanogaster* to aggregate on a resource also attracted parasitoids towards the resources. Consequently, the percentage of larvae that were parasitized was significantly higher in substrates with aggregation pheromone than in control substrates without aggregation pheromone. This indicates that there is an ecological cost to the use of aggregation pheromone. To get a more complete picture of why Drosophila species use chemical information, we will focus on the positive and negative effects of using the Drosophila aggregation pheromone on larval survival and net population numbers of *D. melanogaster* in spatial parasitoid-host model.

We showed that a random dispersing population – that could not use chemical information – was not able to colonize the area that contained the apples. This was mainly because of the high mortality due to the Allee effect. However, also in the simulations without the Allee effect the random dispersing population had more difficulties in colonizing the orchard. This showed that for fruit flies it is essential to use chemical information – especially that from the aggregation pheromone – when colonizing an area. Therewith they are capable of forming aggregations on suitable resources.

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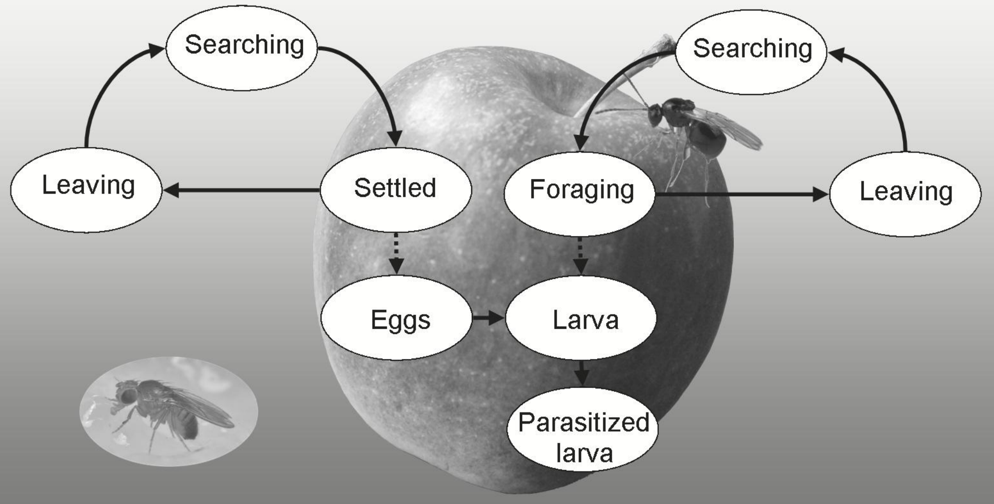

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Chapter 5

A spatio-temporal model with odour-mediated parasitoid-host interactions

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Submitted

Abstract

Chemical information mediates species interactions in a wide range of organisms. Yet, the effect of chemical information on population dynamics is rarely addressed. We designed a spatio-temporal parasitoid-host model to investigate the population dynamics when both the insect host and the parasitic wasp that attacks it can respond to chemical information. The host species, *Drosophila melanogaster*, uses food odours and aggregation pheromones to find a suitable resource for reproduction. The parasitoid, *Leptopilina heterotoma*, uses these same odours to find its hosts. We show that when parasitoids could exploit the chemical information, it negatively affected fruit fly population growth. However, this effect was already present when the parasitoid could only respond to food odours. Our results indicate that the use of the aggregation pheromone by *D. melanogaster* does not lead to an increased risk of parasitism. Moreover, the use of aggregation pheromone by the host enhanced its population growth and enabled it to persist at higher parasitoid densities.

Keywords chemotaxis · aggregation pheromone · Allee effect · competition · parasitoid-host model · infochemicals

5.1. Introduction

Chemical information plays an important role in the biology of many species ranging from microbes to mammals (Bell and Cardé, 1984; Wyatt, 2004; Kats and Dill; 1998, Dicke and Takken, 2006). The so-called infochemicals (Dicke and Sabelis, 1988) can provide information on the availability of food or mates, as well as the presence of competitors or natural enemies. A well-known example of an infochemical is the sex pheromone emitted by female moths that attracts conspecific males over long distances (Wall and Perry, 1987; Ostränd and Anderbrant, 2003). Once the chemicals are released, they are freely available for every organism in the food web (Turlings et al., 1995; Bruinsma and Dicke, 2008). Chemical communication between individuals of one species can potentially be spied upon by a natural enemy (Wiskerke et al., 1993; Hedlund, et al., 1996; Wyatt, 2004; Fatouros et al., 2005). On the other hand, chemical information emitted by predators can also potentially be used by prey animals to avoid or try to escape from predators (Kats and Dill, 1998; Dicke and Grostal, 2001; Fraker, 2008). Most studies on chemical information focus on individuals that respond to chemical cues. Yet, through changes in the behaviour of individuals, chemical mediation of ecological interactions can also play a significant role at the population level (Vet, 1999).

Host-parasitoid interactions can be extensively influenced by the exploitation of chemical information. Chemical compounds emitted by the host can provide searching parasitoids with information on where to find their hosts. Parasitoids often face a problem known as the reliability-detectability problem (Vet and Dicke, 1992). Chemical information emitted by the host is reliable, but usually not well detectable over long distances, as the host is under strong natural selection to be inconspicuous for its natural enemies. Chemicals from the host's habitat are often better detectable over long distances, but this information is not very reliable, because their presence does not necessarily indicate the presence of the host. One way to solve the reliability-detectability problem is to exploit chemicals that hosts emit to communicate with conspecifics, such as sex pheromones or aggregation pheromones (Hedlund et al., 1996; Dicke et al., 1994; Fatouros et al., 2008).

In the present study, we investigate how a natural enemy that eavesdrops on the chemical communication of its host affects the population dynamics of the host. Our study system consists of *Drosophila melanogaster*, the common fruit fly, and its natural enemy, the parasitoid *Leptopilina heterotoma*. This is a generalist parasitoid that attacks the larvae of a variety of *Drosophila* species inhabiting a variety of ephemeral substrates (Janssen et al., 1988). Adult female fruit flies emit a volatile aggregation pheromone (Bartelt et al., 1985) that attracts conspecifics and results in aggregated oviposition by female fruit flies on a suitable resource (Wertheim et al., 2006). *L. heterotoma* parasitoids exploit the aggregation pheromone of the adult fruit flies to localize their hosts, the larvae of the fruit fly (Wiskerke et al., 1993).

Drosophilid fruit flies tend to aggregate on suitable resources. Forming aggregations can benefit individuals in populations that are subjected to an Allee effect (a negative per capita growth rate at small population sizes (Allee, 1931)). If the population density is low, individuals can have difficulties in finding a mate or in exploiting a resource (Wertheim et al., 2005; Berec et al., 2001). For example, a low density can occur when an invading population has to colonize a new area prior to mating. In this situation finding a mate can be difficult and, therefore, there is a higher mortality due to the Allee effect (Robinet et al., 2008). Another possible advantage of aggregation can be a diluted risk of attack by natural enemies at high population densities (the selfish herd theory (Hamilton, 1971)). This can, for instance, be caused by the fact that a predator is only able to attack a certain amount of prey and, thus, more individuals survive at a high prey density, or that a large group of prey is better able to defend itself than a small group. Host finding and egg laying takes time, which limits the amount of eggs a parasitoid can lay in a fixed period of time. On the other hand, forming aggregations can also have costs. Individuals within an aggregation often experience more severe competition for food and mates than when they would be on their own. A large group of individuals can also be more conspicuous to natural enemies and more vulnerable to parasites and diseases (Parrish and Edelstein-Keshet, 1999).

Here, we address the positive and negative effects of using chemical information for intraspecific interactions. For this reason, we mainly focus on the population dynamics of the information-emitting species, *D. melanogaster*. The use of an aggregation pheromone by *D. melanogaster* may affect its population dynamics in three ways. The use of the aggregation pheromone influences two density-dependent effects: the response to the aggregation pheromone promotes the formation of aggregations, which results in a reduction in the mortality due to the Allee effect (Wertheim et al., 2002; Rohlfs et al., 2005; Lof et al., 2009). However, with increasing density, competition increases as well, resulting in larval mortality due to (scramble) competition (Wertheim et al., 2002; Hoffmeister and Rohlfs, 2001; Rohlfs and Hoffmeister, 2003). The third aspect is a side effect of the use of chemical information: namely, the aggregation pheromone used by *D. melanogaster* can be exploited by their natural enemies to locate their host or prey (Wertheim et al., 2003). This may increase the mortality due to predation or parasitism. To study the above effects that chemical information can have on the population dynamics of *D. melanogaster* when there is a parasitoid present that uses the intra-specific communication of *D. melanogaster* to find its host, we have developed a spatio-temporal model that incorporates odour distribution, the behavioural responses of fruit flies and parasitoids. Furthermore, we included a submodel that models the foraging behaviour of the parasitoid and a submodel that calculates the different types of local larval mortality based on local larval density, namely mortality due to the Allee effect due to competition; and the local mortality due to parasitism. In our model, both the parasitoid and the host can respond to chemical information. This is a novel approach, as other models studying the effect of chemical information on the host-parasitoid interaction only consider chemotaxis for the parasitoid and assume random movement by the adult host (e.g. Schofield et al., 2002, 2005; Pearce et al., 2006, 2007).

5.2. Description of the model

We have developed a spatial parasitoid-host model that incorporates infochemical concentration, movement of parasitoids and adults of its hosts (both random and directed towards the infochemical source) and the interactions between the parasitoid and its larval host. In this model, we used difference equations for the fruit fly and parasitoid population dynamics and for the parasitoid-host interactions. The odour distribution and the movement by the parasitoid and fruit flies are based on discretized partial differential equations. The complete model is solved numerically with the integro-difference approach (see appendix I). The fruit fly and parasitoid population and the infochemical distribution are modelled in a two-dimensional environment.

After hibernating in human shelters (Boulétreau-Merle et al., 2003), fruit flies re-colonize an area with suitable breeding sites (i.e. fermenting fruits) at the beginning of the breeding season. At the end of the breeding season they leave the breeding area to find shelter. In the dynamics of this process, we can distinguish separate time scales: 1st, the movement of individual flies, at a scale of minutes up to hours; 2^{nd}, the oviposition and larval development, at a scale of days; 3^{rd}, the generations of fruit flies, at a scale of three weeks; 4^{th}, the population dynamics over one season, at a scale of one year; 5^{th}, the population dynamics over multiple years, at a scale of a decade. In this paper we focus on the 4^{th} scale, the dynamics within one season, because the winter acts as a system reset. The development time from freshly oviposited eggs to adult fruit flies is about 19 days (at 18 °C) (Ashburner et al., 2005). Hence, one breeding season contains about 10 fruit fly generations.

Our simulation model contains 10 non-overlapping fruit fly generations. For each generation, we simulated only seven days: in the first three days the fruit flies disperse and reproduce, and in days 4-7 the parasitoids disperse, search for their hosts and parasitize the fruit fly larvae. In the remaining 12 days of the modelled generation, the unparasitized fruit fly larvae develop into adult fruit flies. We do not simulate this development phase dynamically; instead, we only address the fraction of larvae that survive and constitute the next adult fruit fly population. Within each generation, we treat the total number of adult fruit flies and the total number of adult parasitoids as fixed, i.e. we do not model adult mortality within a generation.

5.2.1 Within-generation adult fruit fly dynamics

In our model, we consider female fruit flies and female parasitoids only. At the start of each generation n, the resources $R(x, y, n, t)$ are placed randomly in the simulated orchard (Box 1 eqn. 1). The female fruit fly population is divided into three subpopulations according to three activities which they can exhibit (Fig. 1). In the air, the searching flies (with density H_C) use chemical information to find a suitable resource, e.g. a yeast-infected apple. On the resource, the settled flies (with density H_S) mate and lay their eggs. In the air, the leaving flies (with density H_L) actively move away from the resource. The equations describing the transitions between all state variables are given in Box 1 eqns. 2-4.

The description of the state variables and the values of the parameters are given in Table 1 (see also **Chapter 3** (de Gee et al., 2008), for an explanation how these parameters were evaluated, and for a sensitivity analysis of the parameters in our model). In eqns. 2-4, α_1, α_2 and α_3 are the rates at which the searching fruit flies settle on a resource, the settled fruit flies leave the resource, the leaving fruit flies start searching for another resource, respectively.

5.2.1.1 Fruit fly dispersal

The presence of infochemicals tends to direct the movement of the searching subpopulations of fruit flies towards the odour source. However, when chemical information is absent, the searching subpopulation can only disperse randomly, with dispersal coefficient D_H, for the searching fruit flies (in last two terms in eqn. 2). The chemotaxis coefficient for the searching fruit flies (ν_H) models the strength of their chemotactic response. Together, dispersion and chemotaxis are modelled as in the last two terms of eqn. 2.

The function $f_H(F, A)$ (Box 1 eqn. 5) is used to model the response of fruit flies to the infochemicals F (food odours) and A (aggregation pheromone). Bartelt et al. (1985) showed that fruit flies have a stronger response to the combination of food odours and

Box 1 Model equations

The simulation is initialized by randomly placing adult female fruit flies in the orchard in generation 1 ($H_C(x,y,1,0)$).

At a start of each new generation *n*, resources are placed randomly on the grid; these are present for the whole generation.

$$R(x,y,n,t) = \begin{cases} 0 & \text{if no apples are present at position } (x,y) \text{ in generation } n, \text{ for all } 0 \le t < 7 \\ 1 & \text{if an apple is present at position } (x,y) \text{ in generation } n, \text{ for all } 0 \le t < 7 \end{cases} \quad (1)$$

During the first 3 days (0≤*t*<3) of generation *n* equations 2-4 hold for the adult fruit fly population,

$$\begin{aligned} H_C(x,y,n,t+\Delta t) &= H_C(x,y,n,t) + \alpha_3 H_L(x,y,n,t)\,\Delta t - \alpha_1 R(x,y,n,t) H_C(x,y,n,t)\Delta t \\ &\quad + D_H \nabla^2 H_C(x,y,n,t)\Delta t - \nabla \cdot \left[\nu_H\, H_C(x,y,n,t) \nabla f_H(F(x,y,n,t), A(x,y,n,t))\right]\Delta t \end{aligned} \quad (2)$$

$$H_S(x,y,n,t+\Delta t) = H_S(x,y,n,t) + \alpha_1 R(x,y,n,t) H_C(x,y,n,t)\,\Delta t - \alpha_2 H_S(x,y,n,t)\Delta t \quad (3)$$

$$H_L(x,y,n,t+\Delta t) = H_L(x,y,n,t) + \alpha_2 K_{ringrandom}(x,y,\Delta t) * H_S(x,y,n,t) - \alpha_3 H_L(x,y,n,t)\Delta t \quad (4)$$

where $*$ denotes the convolution operator. The convolution operator is a short notation for a summation over all spatial coordinates, i.e.:

$$(p*q)(x,y) = \sum_{x'=-\infty}^{\infty} \sum_{y'=-\infty}^{\infty} p(x-x', y-y') q(x', y')$$

Equations 5-8 hold for all 0≤ t<7,

$$f(F(x,y,n,t), A(x,y,n,t)) = \frac{F(x,y,n,t)}{F_0 + F(x,y,n,t)} + \eta \frac{F(x,y,n,t)A(x,y,n,t)}{F_0 A_0 + F(x,y,n,t)A(x,y,n,t)} \quad (5)$$

$$F(x,y,n,t+\Delta t) = F(x,y,n,t) + D_I \nabla^2 F(x,y,n,t)\Delta t + \theta_F R(x,y,n,t)\Delta t - \mu F(x,y,n,t)\Delta t \quad (6)$$

$$A(x,y,n,t+\Delta t) = A(x,y,n,t) + D_I \nabla^2 A(x,y,n,t)\Delta t + \omega A_R(x,y,n,t)\Delta t - \mu A(x,y,n,t)\Delta t \quad (7)$$

$$A_R(x,y,n,t+\Delta t) = A_R(x,y,n,t) + \theta_A H_S(x,y,n,t)\Delta t - \omega A_R(x,y,n,t)\Delta t \quad (8)$$

where, $\theta_A H_S(x,y,n,t)\Delta t = 0$ for $t>3$, because the liquid aggregation pheromone (A_R) is only produced during the egg laying phase of the fruit flies.

During the first three days (0≤*t*<3) of generation *n* the number of fruit fly eggs on the resources are updated by,

$$E(x,y,n,t+\Delta t) = E(x,y,n,t) + \xi H_S(x,y,n,t+\Delta t)\Delta t \quad (9)$$

where $E(x,y,n,0) = 0$ for all $n \in \{1, 2, \ldots, 10\}$

An adult parasitoid generation is initialized at random places in the orchard at day 4 (*t*=3) of each generation *n* ($P_C(x,y,n,3)$). During the last 4 days (3≤*t*<7) of generation *n*, equations 10-17 hold,

$$\begin{aligned} P_C(x,y,n,t+\Delta t) \;=\; & P_C(x,y,n,t) \;+\; \beta_3 P_L(x,y,n,t)\Delta t \;-\; \beta_1 R(x,y,n,t)\, P_C(x,y,n,t)\Delta t \\ & + D_P\, \nabla^2 P_C(x,y,n,t)\Delta t - \nabla\cdot\left[v_P\, P_C(x,y,n,t)\, \nabla f_P(F(x,y,n,t), A(x,y,n,t))\right]\Delta t \end{aligned} \tag{10}$$

$$\begin{aligned} P_F(x,y,n,t+\Delta t) \;=\; & P_F(x,y,n,t) \;+\; \beta_1 R(x,y,n,t) P_C(x,y,n,t)\;\Delta t \\ & -\;(1-\exp(-\beta_{21}\Delta t (N_{tot})^{-\beta_{22}}))P_F(x,y,n,t)\Delta t \end{aligned} \tag{11}$$

$$\begin{aligned} P_L(x,y,n,t+\Delta t) \;=\; & (1-\exp(-\beta_{21}\Delta t (N_{tot})^{-\beta_{22}}))K_{ringrandom}(x,y,\Delta t) * P_F(x,y,n,t)\;\Delta t \\ & + P_L(x,y,n,t) \;-\; \beta_3 P_L(x,y,n,t)\Delta t \end{aligned} \tag{12}$$

Parasitism At the beginning of day 4, all fruit fly eggs (Eqn. 9) are amendable to parasitation,

$$\begin{aligned} & N_{tot}(x,y,n,3) = E(x,y,n,3) = N_u(x,y,n,3) \\ & N_a(x,y,n,3) = 0 \end{aligned} \tag{13}$$

Parasitism of by parasitoids in last four days of generation *n* is modelled by,

$$N_u(x,y,n,t+\Delta t) = N_u(x,y,n,t)e^{-\left(\frac{aP_F(x,y,n,t)\Delta t}{1+at_h N_u(x,y,n,t)}\right)} \text{ for all } 3\le t<7 \tag{14}$$

$$N_a(x,y,n,t+\Delta t) = N_a(x,y,n,t) + N_u(x,y,n,t)\left(1-e^{-\left(\frac{aP_F(x,y,n,t)\Delta t}{1+at_h N_u(x,y,n,t)}\right)}\right) \text{ for all } 3\le t<7 \tag{15}$$

$$N_{tot}(x,y,n,3) = N_{tot}(x,y,n,t) = N_u(x,y,n,t) + N_a(x,y,n,t) \text{ for all } 3\le t<7 \tag{16}$$

The surviving larvae at the end of day 7 constitute to the next generation's (*n* ≥ 1) female adult fruit flies and are calculated by,

$$H_C(x,y,n+1,0) \;=\; \varphi\, N_u(x,y,n,7)\, s_A(N_{tot}(x,y,n,7))\, s_C(N_{tot}(x,y,n,7)) \tag{17}$$

with,

$$\begin{aligned} s_A(N_{tot}(x,y,n,7)) \;&=\; \frac{1}{1+e^{-c_A(N_{tot}(x,y,n,7)-L_A)}}, \\ s_C(N_{tot}(x,y,n,7)) \;&=\; \frac{1}{1+e^{c_C(N_{tot}(x,y,n,7)-L_C)}} \end{aligned}$$

aggregation pheromone than to food odours alone. The fruit flies, however, do not respond to the aggregation pheromone in the absence of food odours (especially yeast odours).

Therefore, we model the response of the searching subpopulations of fruit flies to food odours (with density $F(x,y,n,t)$) and the aggregation pheromone (with density $A(x,y,n,t)$) as a composite Monod function (Monod, 1949; see eqn. 5). In that equation F_0 and A_0 are, respectively, the concentration of food odours and the aggregation pheromone, at which the response is half the maximum. The relative strength of the response to the combination of food odours and the aggregation pheromone as compared to the response to only food odours is described by a parameter η_H for the fruit flies. While the movement of searching subpopulations is directed by chemical information, the movement away from the resource by the leaving subpopulations is not affected by the presence of food odours and the aggregation pheromone. They leave the resource at speed ρ_H in a random direction, dispersing (with diffusivity D_H) for a time t before they start searching for a new resource. After one time step this gives a donut-shaped distribution. In an integro-difference equation it is simulated with a ring-random or 'ripple' dispersal kernel (see Appendix I) (Brewster and Allen, 1997; Allen et al., 2001; Etienne et al., 2002). We chose this type of dispersal to allow for the fact that the majority of the leaving subpopulation actually leaves the resource. If the leaving subpopulation were to use the present chemical gradient, the majority of the fruit flies would immediately return to the same resource that they came from.

5.2.1.2 Fruit fly reproduction

In each generation in our model, all fruit flies lay all their eggs during 3 subsequent days (eqn. 9). Adult females that have settled on a resource, deposit ξ eggs per minute on average. Eggs of *D. melanogaster* develop into larvae after one day and after another day these larvae are susceptible for parasitism by *L. heterotoma*. For simplicity, we assume that the cumulative number of eggs (E) on a resource after 3 days all have developed into unparasitized larvae (N_u) at the start of the fourth day (t=3, eqn. 13).

5.2.2 Odour distribution

D. melanogaster fruit flies respond to food odours (F) and to the aggregation pheromone emitted by recently mated female *D. melanogaster* (A). The female fruit flies do not disseminate the aggregation pheromone as a volatile, but as a fluid accompanying their eggs. We therefore divide the aggregation pheromone into two phases: a liquid or adsorbed form (A_R) on the resource, that slowly evaporates into a volatile form (A) which searching fruit flies and parasitoids can detect in the air. We assume that no wind is present and that these odours thus diffuse randomly, i.e. they spread out in all directions at the same rate. Because odour diffusion is a three-dimensional process, while we model in two dimensions, we introduced a loss term (μ) to represent odour molecules that get out of reach of the searching populations through diffusion in the vertical direction (see Figure 1 in **Chapter 3** (de Gee et al., 2008)). The dynamics of the food odours (F) and the aggregation pheromone (A and A_R) can be found in eqns. 6-8.

5.2.3 Within-generation parasitoid dynamics

As from the fourth day, the larvae that emerged from the eggs are amenable to parasitism. From that moment on, we stop modelling the dynamics of adult fruit fly population and start modelling the dynamics of the female parasitoid population. The parasitoid population is divided into three activity states, similar to the adult fruit flies (eqns. 10-12, Fig. 1). In the air, the searching parasitoids (with density P_C) use chemical information to locate a resource containing their hosts, the larvae of the fruit fly. On the resource, the foraging parasitoids (with density P_F) search for unparasitized hosts to oviposit in. In the air, the leaving parasitoids (with density P_L) actively move away from the resource.

In eqs. 10-12, β_1 and β_3 are the rates at which the searching parasitoids start foraging on a resource, and the leaving parasitoids start searching for another resource respectively. The rate at which the foraging parasitoids leave a specific resource depends on the total number of larvae present on the resource (see eqns. 12-13), $N_{tot}(x,y,n,t)$. The function for this rate is estimated from a study by Van Lenteren and Bakker (1978). They showed that the patch residence time of *L. heterotoma* is related to the number of hosts present on the patch. More specifically, they found that the patch residence time of *L. heterotoma* increased with increasing larval density.

5.2.3.1 Parasitoid dispersal

Analogous to fruit fly dispersal, the dispersal of the parasitoid has coefficient D_P, for the searching parasitoids (in eqn. 10). The coefficient for the strength of their chemotactic response is ν_P.

L. heterotoma has an innate response to the aggregation pheromone, cis-vaccenyl acetate, produced by *D. melanogaster* and some other *Drosophila* species. *L. heterotoma* also responds stronger to the combination of food odours and aggregation pheromone than to food odours alone (Dicke et al., 1985, Wertheim et al., 2003).

We take the shape of the response function $f_P(F(x,y,n,t),A(x,y,n,t))$, and take the values F_0 and A_0, the same as for the fruit flies (Box 1 eqn. 5). For the parasitoids, the relative strength of the response to the combination of food odours and the aggregation pheromone as compared to the response to only food odours is described by the ratio η_P. Members of the leaving subpopulations of parasitoids (Box 1 eqn. 12) first actively fly away from the resource in an arbitrary direction with a speed ρ_P and then disperse randomly, resulting in a ring-random dispersal, just as for the fruit flies (see paragraph 2.1.1 and Appendix I).

Table 1a The state variables involved in odour dispersion and population dynamics

Name	Description
H_C	Searching subpopulation of the fruit flies
H_S	Settled subpopulation of the fruit flies
H_L	Leaving subpopulation of the fruit flies
E	Number of fruit fly eggs on a resource
N_u	Number of unparasitized fruit fly larvae on a resource
N_a	Number of parasitized fruit fly larvae on a resource
N_{tot}	Total number of fruit fly larvae on a resource
A	Concentration of volatile aggregation pheromone
A_R	Concentration of liquid aggregation pheromone emitted by female fruit flies
F	Concentration of food odours released by the resource
P_C	Searching subpopulation of the parasitoid
P_S	Foraging subpopulation of the parasitoid
P_L	Leaving subpopulation of the parasitoid

Table 1b The model parameters involved in odour dispersion and population dynamics, their interactions and their values. For dimensionless parameters the '-' sign is used. All state variables have two spatial coordinates (x, y) and two time variables (n, t).

Name	Description	Value	Units
Δt	Time step for short term population dynamics	5	min
Δx, Δy	Spatial step size	0.1758	m
D_H	Dispersion coefficient of at random moving fruit flies	0.058	$m^2\ min^{-1}$
D_P	Dispersion coefficient of at random moving parasitoids	0.058	$m^2\ min^{-1}$
D_I	Dispersion rate of infochemicals	1	$m^2\ min^{-1}$
α_1	rate at which searching fruit flies settle on a resource	0.25	min^{-1}
α_2	Rate at which settled fruit flies leave the resource	0.002	min^{-1}
α_3	Rate at which moving fruit flies start searching for a resource	0.5	min^{-1}
β_1	Rate at which searching parasitoids settle on a resource	0.25	min^{-1}
β_{21}	Maximum rate at which foraging parasitoids leave the resource	0.188	min^{-1}
β_{22}	Parameter for the density dependence of resource leaving	0.67	-
β_3	Rate at which moving parasitoids start searching for a resource	0.75	min^{-1}
ρ_H	Velocity of movement away from the resource by fruit flies	0.4	$m\ min^{-1}$
ρ_P	Velocity of movement away from the resource by parasitoids	0.1	$m\ min^{-1}$
F_0	Saturation parameter for food odours	10	$ng\ m^{-2}$
A_0	Saturation parameter for the aggregation pheromone	0.04	$ng\ m^{-2}$
μ	Loss rate (including decay) for infochemicals getting out of reach	0.0235	min^{-1}
θ_F	Food odour production by the resource	2	$ng\ apple^{-1}\ min^{-1}$
θ_A	Aggregation pheromone production by settled fruit flies	0.83	$ng\ fly^{-1}\ min^{-1}$
ω	Rate at which liquid aggregation pheromone evaporates	4.10^{-4}	min^{-1}
v_H	Attraction towards infochemicals of *D. melanogaster*	$5D_H$	$m^2\ min^{-1}$
v_P	Attraction towards infochemicals of *L. heterotoma*	$5D_P$	$m^2\ min^{-1}$
κ_H	Relative strength of movement fruit flies towards infochemicals compared to random dispersal	5	-
κ_P	Relative strength of movement parasitoids towards infochemicals compared to random dispersal	5	-
η_H	Relative strength response of *D. melanogaster* to food odours together with aggregation pheromone compared to the attraction to food odours alone	2.51	-
η_P	Relative strength response of *L. heterotoma* to food odours together with aggregation pheromone compared to the attraction to food odours alone	0.35	-
ξ	Egg laying rate of the settled population	0.0083	min^{-1}
a	Searching efficiency of *L. heterotoma* (number of larvae found per parasitoid per time)	0.0073	min^{-1}
t_h	Handling time of *L. heterotoma*	0.3333	min
φ	Sex ratio of the fruit fly larvae (fraction of females)	0.5	-
L_A	Number of fruit fly larvae per apple at which 50 % survives the Allee effect	25	-
L_C	Number of fruit fly larvae per apple at which 50% survives scramble competition	250	-
c_A	Slope sigmoid survival curve modeling the Allee effect	0.088	-
c_C	Slope sigmoid survival curve modeling the competition	0.044	-

5.2.3.2 Parasitism

We modelled parasitism on a resource by the foraging subpopulation ($P_F(x,y,n,t)$) as a Holling type II functional response (Holling, 1959), which accounts for a saturating maximum parasitism rate (eqns. 14-16). Here, $N_u(x,y,n,t)$ is the number of unparasitized larvae on a resource, $N_a(x,y,n,t)$ is the number of parasitized larvae on a resource, and $N_{tot}(x,y,n,t)$ is the total number of larvae on a resource, a is the search efficiency of *L. heterotoma* and t_h is the handling time, i.e. the time between detecting a host and subsequently resuming the search for another host.

5.2.4 Between-generation population dynamics: Survival of the fruit fly larvae

If we neglect parasitism for a moment, two density-dependent mortality factors affect local larval *D. melanogaster* survival. Mortality due to competition plays a role at high densities, while at low densities mortality due to the Allee effect is more important. In *D. melanogaster* the Allee effect arises from invasion of the resources by fungi (Rohlfs et al., 2005; Rohlfs, 2006). The presence of adult fruit flies on a resource before egg-laying has a positive effect on overcoming this fungal colonization. With increasing density, chances for fungal invasion decrease, which constitutes the Allee effect. Adult *D. melanogaster* inoculate the resource with yeasts (Morais et al., 1995). This has two beneficial effects: first, it increases the amount of food for the larvae and, thus, makes exploiting the resource easier. Second, yeast competes with the fungi, reducing fungal growth. This is beneficial because fungi may cause a high mortality of fruit fly larvae when the larvae are present in low numbers (Rohlfs et al., 2005; Rohlfs, 2006). The fraction of the larvae that survive on a resource is highest for intermediate larval densities (Box 1 Eq. 17). We assume that parasitism does not affect the behaviour of *Drosophila* larvae, and that the Allee effect and competition affect parasitized and unparasitized larvae equally.

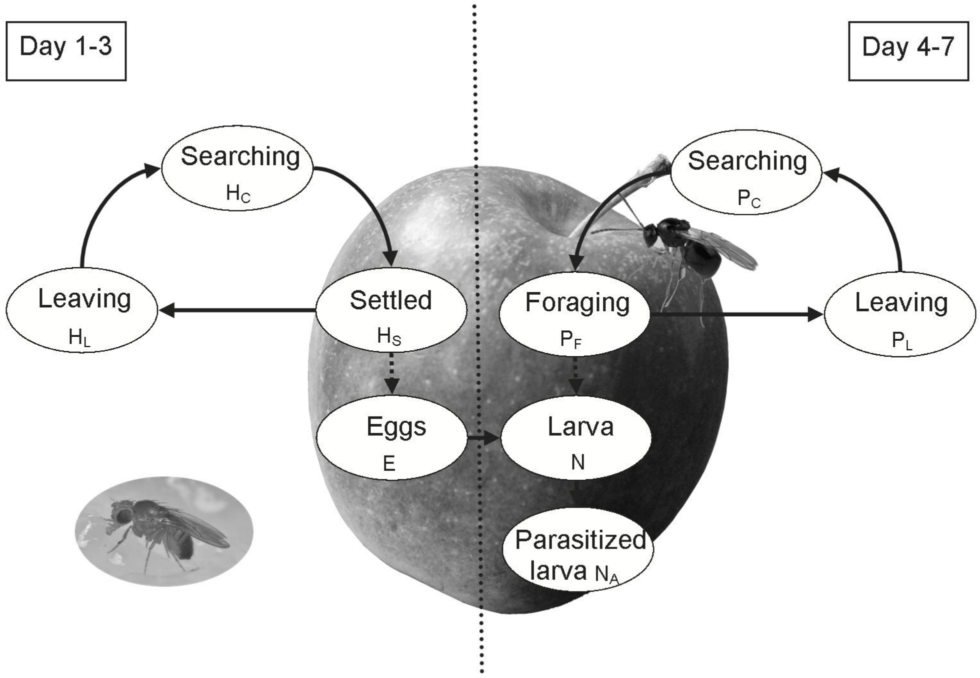


Figure 1 Schematic representation of the population dynamics. The fruit fly population is divided into three activity states; H_C the searching part fruit fly population in the air, H_S the settled part of the fruit fly population that lays eggs on the resource, H_L the part of the fruit fly population that just left the resource. The parasitoid population is also divided into three activity states; P_C the searching part of the parasitoid population in the air, P_F the foraging part of the parasitoid population that lays their eggs in the larvae of the fruit fly, and P_L the part of the parasitoid population that decided to leave the resource. Each generation we model 7 days. From day 1 to 3 the fruit flies disperse and lay eggs on the resource. At the beginning of day 4, all eggs are developed into larva that can be parasitized by the parasitoid from day 4 to 7. Pictures Hans Smid (Bugsinthepicture.com).

Therefore, we calculate the fraction that survives the Allee effect (s_A) and the fraction that survives competition (s_C) of all the larvae (N_{tot}) (Eq. 17). Unparasitized larvae that survive the Allee effect and competition develop successfully into adult fruit flies. Of the surviving larvae, a fraction φ is female and these constitute the next adult female generation (generation n +1). Resources are ephemeral and the position of the resources varies randomly between generations. We assume that adults emerge *in situ* from their pupa and will immediately start searching for a suitable resource. Thus, all the surviving larvae start in the searching subpopulation in the next generation.

5.2.5 Between-generation population dynamics: Parasitoids

The development from larvae to newly emerged adults is not always synchronized between parasitoid and host (Godfray, 1994). In our system, the development time for *L. heterotoma* is approximately 3 times longer than for *D. melanogaster*. Therefore, the surviving parasitized larvae do not directly constitute the next generation's parasitoid population. There is a delay in time of approximately two fruit fly generations before the parasitoids develop into adults. Following parasitoid populations would be an interesting model extension but it would require a division of the parasitoid population in multiple active and inactive age classes and keeping track of their spatial distribution. Spatial parasitoid-host models that include the response to chemical information often either assume overlapping generations (Schofield et al., 2005, Pearce et al., 2007), have simplified population dynamics of the host (Schofield et al., 2002), or do not model the complete population dynamics of the parasitoid (Puente et al., 2008). In this study we are interested in the costs and benefits of communicating through an aggregation pheromone for fruit fly population dynamics. Therefore, we chose not to model parasitoid reproduction explicitly. Instead, we started each generation with a fixed number of parasitoids, that were randomly placed in the area. We also studied the effect of a parasitoid population that fluctuates in time. For these simulations we set the number of parasitoids at the beginning of a generation equal to a fixed fraction of the adult fruit fly population and assumed a random initial distribution. This simple solution was based on the fact that *L. heterotoma* is a generalist parasitoid, attacking more than one host species.

5.3. Simulation set-up

We considered a spatial domain of 90 m × 90 m. This was divided into 512×512 cells with side length of 0.1758 m. To eliminate possible boundary effects, we enlarged the simulated area to 180 m × 180 m, with the actual domain in the centre. On this enlarged domain, we used periodic boundaries for the odour distribution and for the fruit fly and parasitoid population. We ran simulations for one breeding season, consisting of ten discrete generations. Per generation, we simulated three dispersal/reproduction days for the fruit fly population followed by 4 dispersal/oviposition days for the parasitoid population, each day consisting of twelve hours, divided in time steps (Δt) of 5 minutes (Fig. 2). Non-volatile aggregation pheromone is only excreted by the fruit flies in the first 3 days of the generation; thereafter there is only evaporation of the non-volatile form that is still present on the resource. Food odours are produced during all 7 simulation days. At the end of our modelled generation it takes another 12 days for the unparasitized larvae to develop into adult fruit flies. We do not model this development explicitly, instead, we only look what fraction of the larvae survive and constitute the next adult fruit fly population. Within each generation, the total number of adult fruit flies and the total number of adult parasitoids is kept constant, i.e. we do not model adult mortality within a generation.

We studied the effect of the ability to use chemical information by both fruit flies and their parasitoids on the population dynamics of the fruit fly by comparing the fruit fly abundance and persistence for 5 different combinations of response types to chemical information: fruit flies that disperse randomly (0) or can use both food odours and aggregation pheromone (FA), combined with parasitoids that disperse randomly (0), use food odours (F) or use both food odours and aggregation pheromone (FA). This can be combined into 6 different combinations. However, when parasitoids could use food odours and aggregation pheromone, we only looked at the combination where fruit flies could do so too. So we did not model the combination where the parasitoid could use both odours (FA) while the fruit flies could not use chemical information (0). For the simulations with a fixed number of parasitoids present, we compared the population dynamics of the fruit flies when 0, 300, 500, 700 or 900 parasitoids were present in the orchard. In the simulations where the number of parasitoids at the beginning of a new generation was a fixed fraction of the number of fruit flies present, the population size of the parasitoids was 0.125 times the size of the fruit fly population.

In the centre of the domain, we simulated an orchard of 60 m × 60 m with abundant resources (1 apple m^{-2}). To mimic the natural situation, new apples were randomly allocated for each new generation of flies. At the beginning of the simulation we released 4,000 adult fruit flies, randomly distributed in the orchard. We ran each simulation three times with different random resource distributions to verify the consistency of the results.

To investigate the implications of using chemical information by the fruit fly while a natural enemy spies upon this information, we compared the percentage mortality of the fruit fly larvae due to the Allee effect, due to competition and due to parasitism for the different combinations of response to chemical information by the fruit fly and the parasitoid. With a model approach we can specifically investigate what mortality factor ("Allee effect", "competition" or "parasitism") or combination of mortality factors ("parasitism and Allee effect" or "parasitism and competition") caused the fruit fly larvae mortality. We investigated whether the formation of aggregations by the fruit flies in response to the aggregation pheromone resulted in a diluted risk of parasitism.

5.3.1 Statistics

We used linear mixed models to test the effect of the use of infochemicals on the percentage mortality due to the Allee effect, percentage mortality due to competition, percentage mortality due to parasitism and the total number of fruit flies in the orchard. We used an arcsine square root transformation for the percentage mortality due to the Allee effect, due to competition and due to parasitism and a logarithmic transformation for the total number of fruit flies in the orchard, because the values in the latter varied over several orders of magnitude.

The linear mixed effect model is especially suitable for data where the measurements are correlated in time. In the model we used "generation" as repeated measurement, and "treatment", "generation" and "treatment x generation" as fixed effects. We tested the model for four different covariance structures, compound symmetry (CS), first-order autoregressive (AR(1)), heterogeneous first-order autoregressive (ARH(1)) and an unstructured covariance matrix (UN). We found that AR(1) was the best model for the data (it had the lowest AIC). For these statistics we used SAS 9.1.

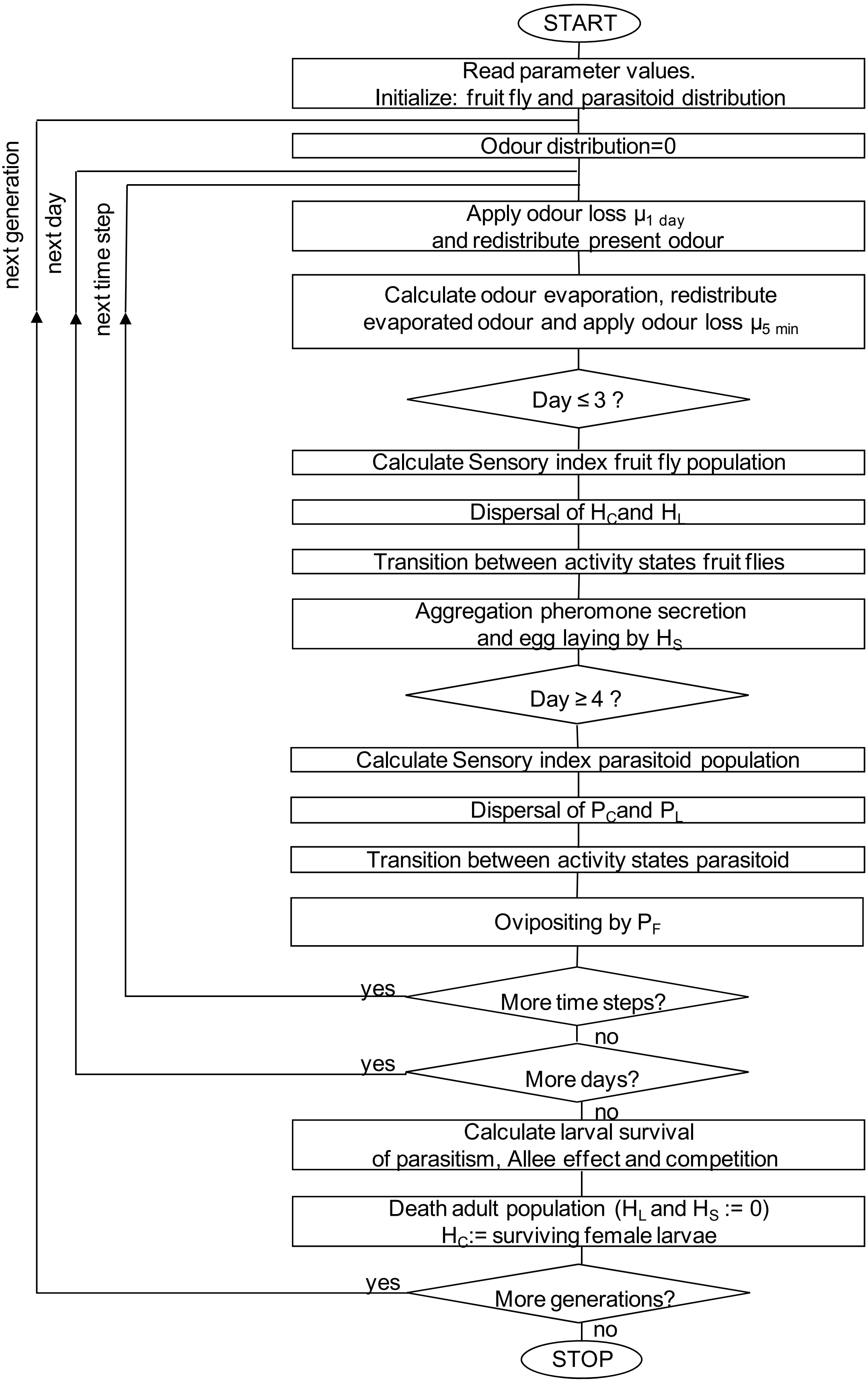


Figure 2 Flow chart of the processes in the model. In our model, the time step, Δ*t*, is 5 min. We simulated10 generations, each generation consisted of 7 simulation days.

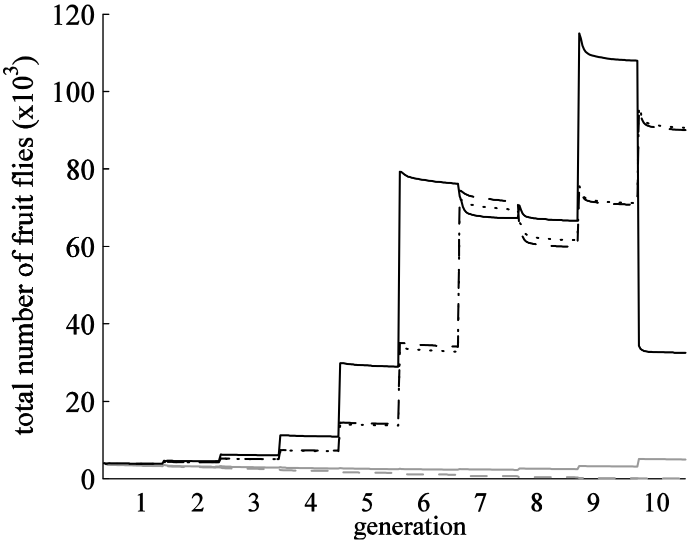


Figure 3 The dynamics of the total fruit fly population in the orchard (60m × 60m), for all 10 generations. The simulations were run with a fixed total number of parasitoids; 500 each generation. The five lines represent the following situations: Dm 0 Lh 0 solid gray line; Dm 0 Lh F dashed gray line; Dm FA Lh 0 solid black line; Dm FA Lh F dashed black line; Dm FA Lh FA dotted black line

5.3.2 Diluted risk of parasitism attack

To test whether there is a diluted risk of parasitism, we studied the percentage mortality due to parasitism per resource, and investigated how it relates to larval density. If there is a diluted risk of parasitism we expect that the percentage mortality due to parasitism decreases with local larval density. To test whether the ability to use chemical information affects the risk of parasitism, we studied the local percentage parasitism for the five combinations of infochemical use by the fruit flies and *L. heterotoma*. We also studied whether there are differences in the density-dependent percentage parasitism between the simulations with a fixed number of parasitoids (500) and a fixed fraction of parasitoids (1 adult parasitoid per 8 adult flies).

5.4. Results

5.4.1 Effect of infochemical use at fixed parasitoid density

The use of infochemicals by the fruit flies has a positive effect on their population growth. The total number of fruit flies in the orchard in the first six generations increases significantly faster when fruit flies can respond to chemical information ($P<0.0001$) (Fig. 3). Furthermore when fruit flies were not able to use chemical information the population went towards extinction in all replicates when the parasitoids were able to use food odours, and in two out of three replicate simulations when the parasitoids were not able to use chemical information. Counter-intuitively, this was not caused by parasitism, as the percentage mortality due to parasitism was significantly lower when fruit flies could not respond to chemical information ($P<0.0001$). Instead, it was mainly caused by the higher percentage mortality due to the Allee effect ($P<0.0001$) (Fig. 4a).

The use of infochemicals by the parasitoids had a negative effect on the growth of the fruit fly population. When fruit flies could not respond to chemical information, the ability to use food odours by the parasitoids caused a stronger decrease of the fruit fly population ($P=0.029$). For fruit flies that could use chemical information, the population growth was significantly slower when parasitoids also could use chemical information than when parasitoids moved randomly ($P<0.0001$). There was no difference in fruit fly population growth between simulations with parasitoids using both fruit odours and aggregation pheromone and parasitoids using only food odours ($P=0.36$).

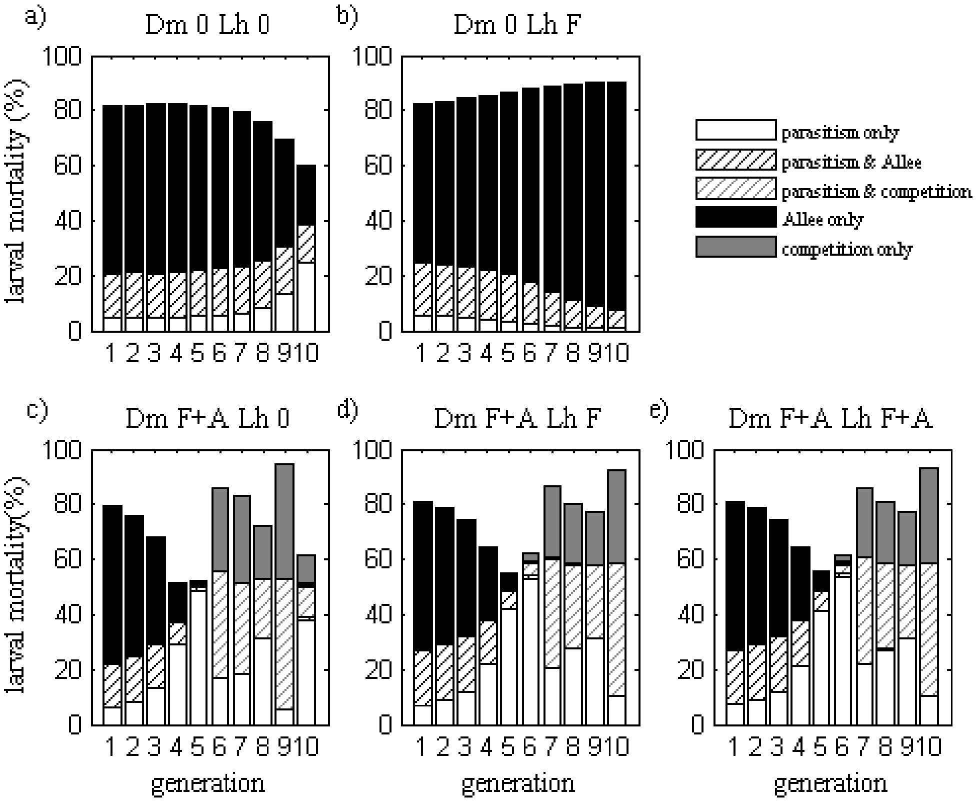


Figure 4 Local percentage mortality of fruit fly larvae per generation (a) Dm 0 Lh 0, (b) Dm 0 Lh F, (c) Dm FA Lh 0, (d) Dm FA Lh F, and (e) Dm FA Lh FA. The simulations were run with a fixed number of 500parasitoids each generation.

5.4.2 Percentage mortality of larvae at fixed parasitoid density

The ability of the fruit flies to use chemical information affects the mortality of their offspring. When fruit flies could respond to chemical information there was a significant trend in time in the first 5 generations: the percentage larval mortality due to the Allee effect decreased significantly ($P<0.0001$) (Fig. 4c-e) while the percentage mortality due to parasitism increased significantly ($P<0.0001$) (Fig. 4c-e), both effects are mainly caused by the increasing population size. After the fifth generation larval competition increased so strongly that it impeded further population growth (Fig. 4c-e). When fruit flies were not able to respond to chemical information no significant trend in time was observed for percentage larval mortality due to the Allee effect or competition (Fig. 4a-b).

The use of chemical information by the parasitoids negatively affects the percentage larval mortality of the fruit flies. When both parasitoids and fruit flies could use chemical information the average percentage parasitism was slightly higher in the first 4 generations (Fig 4c-e). This slowed down population growth, and thereby the percentage mortality due to the Allee effect remained higher ($P<0.0001$). Again, there was no difference in percentage larval mortality between the simulation where parasitoids responded to food odours only or to the combination of food odours and aggregation pheromone (Fig 4d-e). When fruit flies were not able to respond to chemical information, no significant effects of the use of infochemicals by the parasitoids were observed.

5.4.3 Effect of parasitoid density

The number of parasitoids in the orchard affected the fruit fly persistence. When fruit flies could not use chemical information, the population could only persist at low parasitoid densities, while fruit flies that could use chemical information could co-exist in the presence of a larger parasitoid population (Table 2). The presence of more parasitoids delayed the population growth (Fig. 5). This was mainly caused by the fruit fly population needing more time to overcome the Allee effect due to higher parasitism. The use of infochemicals by the parasitoids delayed the population growth even more. When parasitoids could use chemical information, more parasitoids settled on a resource and thus more larvae were parasitized.

5.4.4 Effect of infochemical use for a fixed fraction of parasitoids

When the number of parasitoids present in the orchard was a fixed fraction of the number of fruit flies – i.e. 0.125 times the fruit fly population size – this had a large effect on the fruit fly population size and population dynamics (Fig. 6). The maximum population size was much smaller when the parasitoid numbers were fixed per generation. Strikingly, the fruit fly population was not only smaller when parasitoids could use chemical information, but also when parasitoids searched randomly. Furthermore, the fruit fly population was more stable, i.e. the population fluctuations were smaller when a fixed fraction of parasitoids was used in each generation. This was because the competition threshold for mortality (Box 1 eqn. 18) was not reached. The use of chemical information by parasitoids has a negative effect on fruit fly population growth and size. Both when fruit flies could use chemical information and when they dispersed randomly, the population size in the first five generations was significantly lower when parasitoids could also use chemical information (FA: $P<0.0001$; 0: $P=0.0008$). Moreover, after the 5th generation the fruit fly population size was significantly smaller when parasitoids could also use chemical information ($P<0.0001$).

On the other hand, the ability to use chemical information by the fruit flies had a positive effect on their population growth (Fig. 6), as was also the case when the parasitoid numbers were fixed. When both fruit flies and parasitoids were unable to use chemical information, however, the fruit fly population can persist and reach high population numbers. When parasitoids were able to use chemical information, the randomly dispersing fruit fly population went towards extinction in two out of three replicates.

5.4.5 Percentage mortality of larvae at fixed fraction of parasitoids

The use of chemical information by both fruit flies and parasitoids had an effect on the percentage mortality due to the Allee effect and due to parasitism (Fig. 7). When fruit flies could use chemical information, the percentage mortality as a result of the Allee effect was significantly lower ($P<0.0001$) but at the same time there was a significantly higher percentage mortality due to parasitism ($P<0.0001$). Both effects are directly linked to the fact that the fruit fly population was larger. In contrast, the ability to use chemical information by the parasitoids delayed the fruit fly population growth resulting in a significantly higher percentage mortality due to the Allee effect in each generation (FA: $P<0.0001$; 0: $P=0.023$). The average percentage parasitism was higher when parasitoids were able to use chemical information (FA: $P=0.004$, 0: $P=0.0201$).

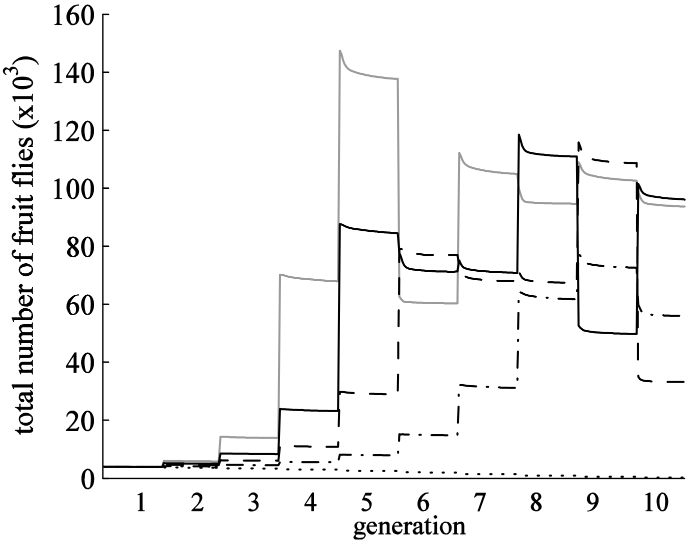


Figure 5 The dynamics of the total fruit fly population in the orchard (60m × 60m), for all 10 generations, when fruit flies could use both food odours and aggregation pheromone and parasitoids could not use chemical information for a fixed number of parasitoids: 0 (solid gray line), 300 (solid black line), 500 (dashed line), 700 (dashed dotted line), or 900 (dotted line) parasitoids each generation.

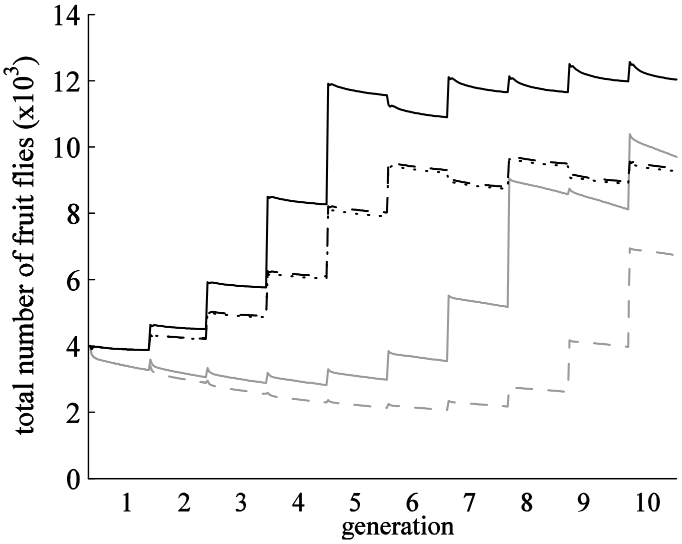


Figure 6 The dynamics of the total fruit fly population in the orchard (60m × 60m), for all 10 generations. The simulations were run with a variable total number of parasitoids, i.e. 0.125 times the total fruit fly population for each generation. Dm 0 Lh 0 solid gray line; Dm 0 Lh F dashed gray line; Dm FA Lh 0 solid black line; Dm FA Lh F dashed black line; Dm FA Lh FA dotted black line.

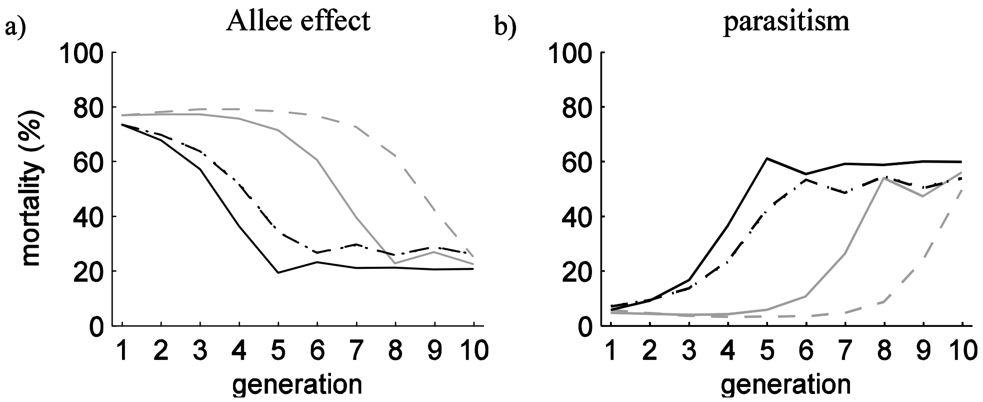


Figure 7 Larval mortality due to (a) the Allee effect, and (b) parasitism for all ten generations. The simulations were run with a variable total number of parasitoids, i.e. 0.125 times the total fruit fly population for each generation. Dm 0 Lh 0 solid gray line; Dm 0 Lh F dashed gray line; Dm FA Lh 0 solid black line; Dm FA Lh F dashed black line; Dm FA Lh FA dotted black line (same trajectory as dashed line).

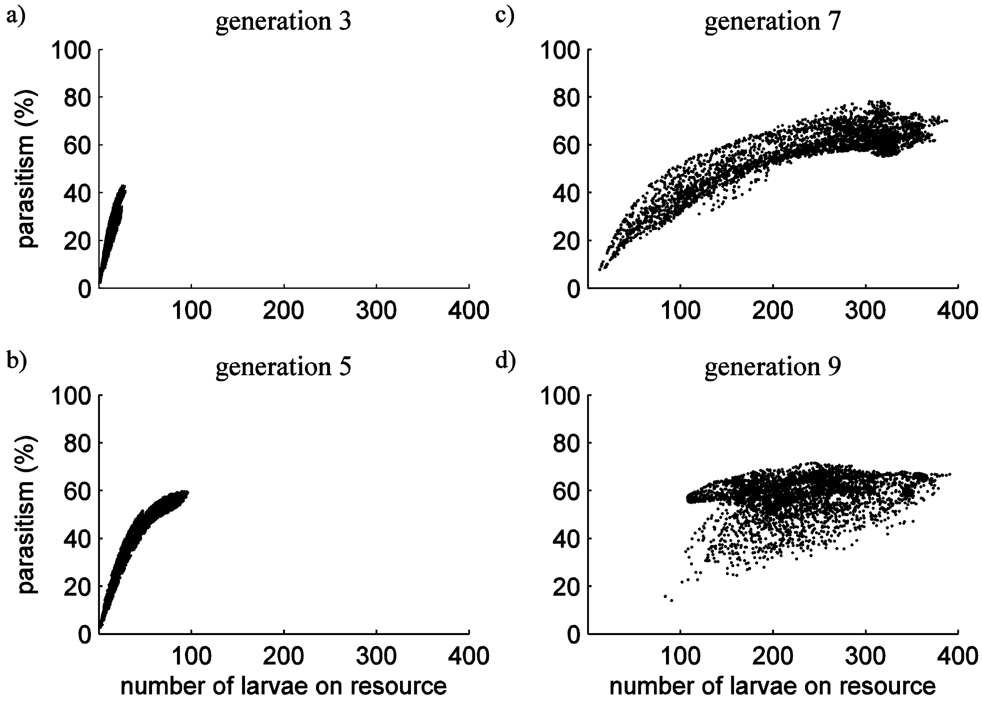


Figure 8 Larval mortality due to parasitism for each resource depicted for larval density on resource in simulations with a fixed number of 500 parasitoids; each generation. Depicted are generation (a) 3, (b) 5, (c) 7, and (d) 9 for the simulations where both fruit flies and parasitoids could respond to both food odours and aggregation pheromone (Dm FA Lh FA).

However, the effective parasitism (as depicted in Fig. 7) was significantly lower when parasitoids could use chemical information (FA: $P<0.0001$, 0: $P=0.017$). This can be explained by the higher percentage mortality due to the Allee effect when parasitoids use chemical information, which also caused higher percentage mortality in parasitized larva resulting in less larvae dying only due to parasitism.

5.4.6 Diluted risk of parasitism?

We did not find a diluted risk of parasitism for higher numbers of larva per resource. On the contrary, we found that percentage parasitism increased with increasing numbers of fruit fly larvae on a resource (Fig. 8). The increase of percentage parasitism with number of larvae present on a resource occurred for all simulations. However, when the number of parasitoids was fixed we found more variation in percentage parasitism after the strong population growth of the host (Fig 8 c-d). This indicates that even though there is locally no diluted risk of parasitism, global dilution of risk exists when not enough parasitoids are present to parasitize all larvae. Handling a host and laying an egg costs time (30 seconds for *L. heterotoma* (Wertheim et al., 2001)). When many larvae are present the handling time sets the upper limit to how much larvae *L. heterotoma* can parasitize in a fixed time interval. Therefore, it could not reach the same high percentage parasitism at all resources. When the number of parasitoids was fixed, and the fruit fly population was large, we found high percentage parasitism only in a part of the resources. When the number of parasitoids was a fixed fraction of the fruit fly population, there was no increase in the variation in percentage parasitism when the fruit flies reached their carrying capacity. A possible explanation may be that there were fewer fruit fly larvae per resource (maximum 70) and at these local densities there was not much variation in percentage parasitism in the simulations with a fixed number of parasitoids either. However, another possible explanation is that at the chosen ratio parasitoids to fruit flies there are sufficient numbers of parasitoids to exploit all resources and in this situation they are not time-limited. In fact, we found that, for a fixed fraction of parasitoids, percentage parasitism was at the same larval densities 10 to 20% higher than in the simulations with a fixed number of parasitoids. This indeed indicates that the parasitoids had enough time to exploit all resources efficiently.

5.5. Discussion

The response of insects to chemical information has been studied in great detail both in the laboratory and in the field (reviewed in Bell and Cardé, 1984; Kats and Dill, 1998; Dicke and Grostal, 2001; Wertheim et al., 2005; Fatouros et al., 2008). Predators and parasitoids commonly use chemical cues associated with herbivore feeding (upon infestation many plants produce volatiles that are attractive to predators and parasitoids) and cues that are associated with reproduction (for instance sex-pheromones of their prey) to locate prey (Turlings et al., 1995; De Moraes et al., 1998; Shiojiri et al., 2001; De Boer and Dicke, 2004; Fatouros et al., 2005; Bruinsma and Dicke, 2008). The exploitation of chemical cues of the host or the host's habitat by predators or parasitoids often results in a higher attack or parasitism rate (Wertheim et al., 2003; but see Tentelier and Fauvergue, 2007). However, to our knowledge, the consequences of the ability to use chemical information on population dynamics have not been addressed in a modelling study in a system where both parasitoid and host can respond to the same chemical information. Several modelling studies addressed parasitoid-host dynamics in a system where only the movement of the parasitoids was influenced by chemical information (Puente et al. (2008), Schofield et al. (2005), Pearce et al. (2007)).

Effects of the use of chemical information by host

Consistent with previous studies (Lof et al., 2008, 2009), we found that the use of chemical information by the fruit flies enhanced their own population growth rate, even when parasitoids are present. In addition, in the present study we found that fruit flies that use chemical information, i.e. food odours and the aggregation pheromone, could persist with more parasitoids present than in the situation where they only dispersed randomly. When fruit flies used chemical information, more fruit flies found the resources. Therefore, more eggs were laid per resource, resulting in a lower percentage mortality due to the Allee effect. Through this reduction in percentage mortality due to the Allee effect, the population was able to survive higher parasitism pressure.

Effects of spying parasitoids

In the present study, we have shown that the ability to use chemical information by both parasitoid and host affects the population dynamics of the host. In accordance with experimental results of Wertheim et al. (2003) for the same experimental system, we found that when parasitoids exploited chemical information the average percentage parasitism was higher. As a result, the population growth rate of the fruit flies was lower. Therefore, it took longer to overcome the negative effects associated with a small population density – i.e. the Allee effect. Furthermore, this negative effect was stronger when fruit flies were not able to use chemical information and had to find the resources by random dispersal. Protection from predators is viewed as an important selective advantage to being a group member in an aggregation (Parrish and Edelstein-Keshet, 1999). In our modelling study we found no local diluted risk of parasitism at higher larval densities. Instead, we found that percentage mortality of larvae due to parasitism increased with larval density on a resource.

Ecological costs of chemical communication

Predation and parasitism are important mortality factors for many insect herbivores. Predators and parasitoids often use chemical information to locate their prey or hosts. This is especially advantageous for natural enemies that search for cryptic prey. Predation and parasitism are expected to exert a strong selective pressure on intra-specific communication by chemical information. Nevertheless, as pheromones are crucial to many aspects of herbivore life history, radical alterations of these compounds could be disadvantageous despite their exploitation by predators and parasitoids (but see Raffa et al., 2007).

In *Drosophila*, larval parasitism is an important mortality factor (Janssen et al., 1988; Allemand et al., 1999; Wertheim et al., 2003; Fleury et al., 2004). The larval parasitoid *L. heterotoma* exploits the aggregation pheromone of the adult fruit flies to localize its hosts. We, therefore, expected that the use of aggregation pheromone by *D. melanogaster* would increase the percentage mortality due to parasitism in the larvae of *D. melanogaster*, as was also found in the field (Wertheim et al., 2003). However, we did not find evidence for an ecological cost for the use of aggregation pheromone by *D. melanogaster* to aggregate on suitable resources with respect to increased risk of parasitism. We found no significant differences in the percentage mortality of fruit fly larvae and fruit fly population size between the simulations where parasitoids could only use food odours on the one hand and the simulations where they could also exploit the aggregation pheromone of *D. melanogaster* on the other hand. However, this does not imply that there is no cost with respect to parasitism when parasitoids can respond to chemical information. The fruit fly population increased at a slower rate (both for the fixed number and the fixed fraction of parasitoids) and had a lower carrying capacity (only at a fixed fraction of parasitoids) when parasitoids could use chemical information as compared to the simulations where they could only search randomly. This, however, is already the case when parasitoids could only respond to food odours. In this respect, the risk of parasitism by *L. heterotoma* responding to food odours is comparable to the risk of parasitism in a system where parasitoids exploit herbivore-induced plant volatiles (DeMoreas et al., 1998) or odours from microbial symbionts (Boone et al., 2008) to locate their hosts. It is important to note that the presence of food odours is not something that the fruit flies are likely to ‘control’.

Appendix I

In the numerical solution of the model equations, the odour diffusion and fruit fly dispersal was treated separately from the adult fruit fly population dynamics. Odour distribution, odour evaporation and movement by the fruit fly and parasitoid populations were solved using the integro-difference (IDE) approach (as in Neubert et al., 1995, Powell et al., 1998). In this approach, dispersion is treated as a separate process. The analytical solution of this process is used in the simulation model. This is an effective approach, because it allows us to take large time steps, without running into any numerical stability problems.

Odour distribution and odour evaporation

The distribution of odours is calculated by taking the convolution product of the odour density and the probability density function, or dispersal kernel (denoted by K_{random}), for random diffusion, described by

$$K_{random}(x,y,\Delta t) = \frac{1}{4\pi D\Delta t} e^{-\frac{x^2+y^2}{4D\,\Delta t}} \tag{A.1}$$

where Δt is the time step taken, with $D=D_I$, the diffusion constant of the infochemicals.

During each time step, food odours and the aggregation pheromone evaporate into the air. The dispersal of the produced odour is calculated by taking the convolution product of the odour produced per minute and a dispersal probability function for a continuously producing source. The distribution of the produced odour is described by

$$K_{evaporation}(x,y,\Delta t) = \int_0^{\Delta t} \frac{1}{4\pi D_I t} e^{-\frac{x^2+y^2}{4D_I t}} \, dt \tag{A.2}$$

Ring random dispersal

Ring random dispersal, used to model the movement away from the resource of the leaving populations (H_L, P_L), is described by

$$K_{ringrandom}(x,y,\Delta t) = \frac{1}{4\pi D\Delta t} e^{-\frac{(\sqrt{x^2+y^2} - \rho\Delta t)^2}{4D\Delta t}} \tag{A.3}$$

where ρ is the velocity of the displacement away from the resource. Fruit flies fly away with velocity $\rho=\rho_H$ and parasitoids with $\rho=\rho_P$. Furthermore, D is the diffusion constant of the leaving population, with $D=D_H$, for the leaving fruit flies or $D=D_P$ for the leaving parasitoids.

Chemotactic movement

In order to implement the chemotactic movement in an IDE approach, the changes in the spatial distribution of searching fruit flies (Box 1, Eqn. 2) and searching parasitoids (Box 1, Eq. 11) due to chemotaxis and random dispersal are approximated by transforming (as in Powell et al., 1998) the general chemotaxis and diffusion equation with W either equal to P_C or H_C as given in A.4 into A.5.

$$W(x,y,t+\Delta t) = W(x,y,t) + D\nabla^2 W(x,y,t)\Delta t - \nabla \cdot \left[v W(x,y,t) \nabla f \right] \Delta t \tag{A.4}$$

$$\widetilde{W}(x,y,t+\Delta t) \;=\; \widetilde{W}(x,y,t)+D\nabla^2\widetilde{W}(x,y,t)\Delta t \;+\; v\nabla f\cdot\nabla\widetilde{W}(x,y,t)\Delta t\,, \tag{A.5}$$

For this, we made a change of variables with A.6.

$$\widetilde{W}(x,y,t)=\exp\left[-\frac{v}{D}f\right]W(x,y,t)\,. \tag{A.6}$$

Subsequently, $\widetilde{W}(x,y,t)$ is expanded using a truncated series approximation,

$$\widetilde{W}(t)\approx\sum_0^i v^i\widetilde{W}_i(x,y,t) \tag{A.7}$$

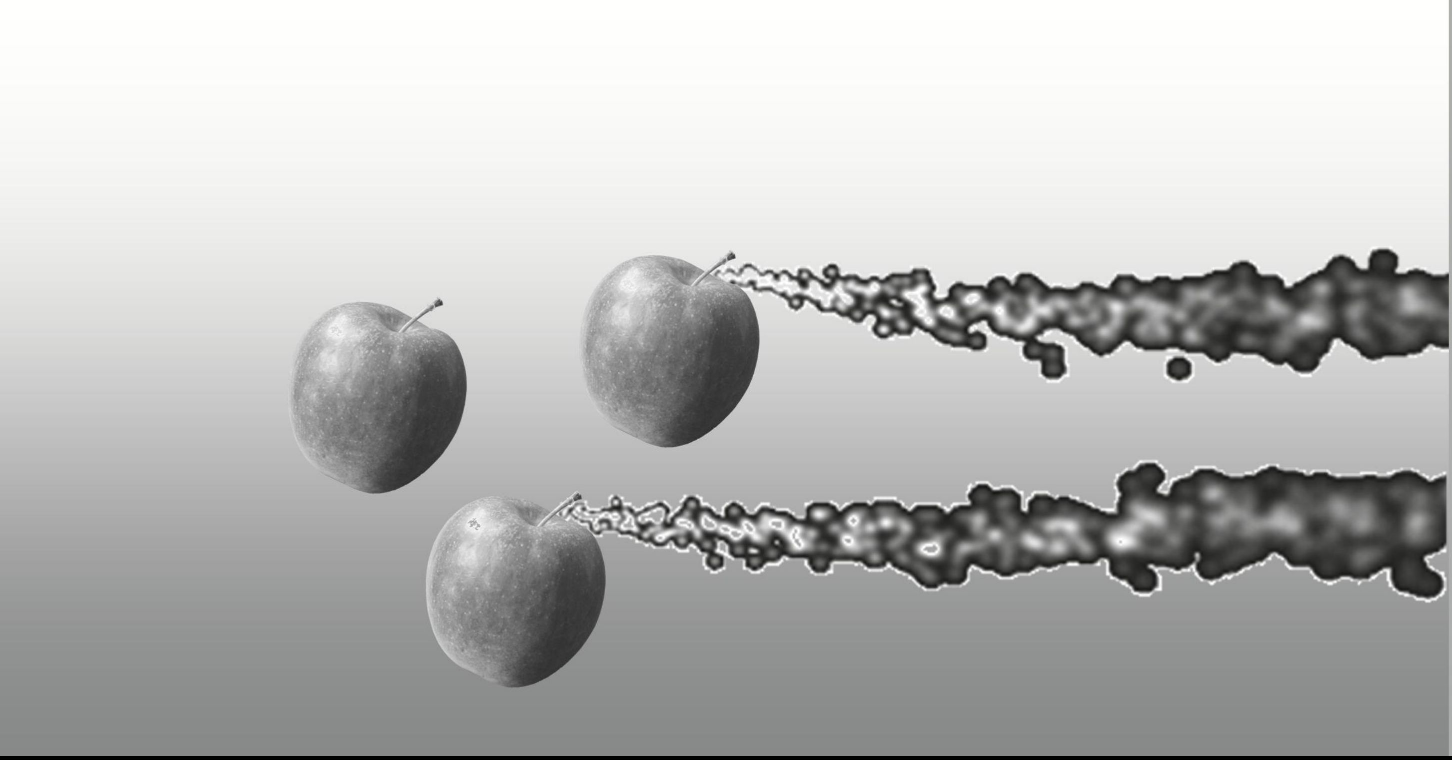
with,

$$\begin{aligned}&\widetilde{W}_0(x,y,t)=K_{random}(x,y,t)*\widetilde{W}_0(x,y,0)\\&\widetilde{W}_i(x,y,t)=\int_0^t K_{random}(x,y,t-T)*\left[\nabla f\cdot\nabla\widetilde{W}_{i-1}(t)\right]dT\,,\quad \mathit{for}\ i\geq 1,\widetilde{W}_i(x,y,0)=0\end{aligned} \tag{A.8}$$

Here K_{random} denotes the kernel function for random dispersion (Eqn. A.1), with D=D_H, for the searching fruit flies or D=D_P for the searching parasitoids, and * denotes the spatial convolution, which is evaluated using a fast Fourier transform (FFT). The integral over time is approximated numerically with Simpson's rule. Finally, the resulting approximation for $\widetilde{W}(x,y,t)$ is transformed back using A.9.

$$W(x,y,t+\Delta t) \;=\; \widetilde{W}(x,y,t+\Delta t)\cdot\exp\left(\tfrac{v}{D}f\right) \tag{A.9}$$

For W we substitute either the searching subpopulation of the parasitoids, P_C, or the searching subpopulation of the fruit flies, H_C. Consequently, for v and D we substitute v_H and D_H for the searching fruit flies (Box 1, Eqn. 2) and v_P and D_P for the searching parasitoids (Box 1, Eqn. 11).



Picture Marjolein Lof

Chapter 6

Searching for a suitable resource

Modelling decision rules of *Drosophila melanogaster* during odour plume tracking

Marjolein E. Lof, Maarten de Gee, Bregje Wertheim, Lia Hemerik

Abstract

Many insects use volatile chemical cues to gather information about their environment. As the wind disperses odour molecules from the source, these infochemicals are distributed into the environment. The structure of an odour plume is complex and varies with time. At a large scale, the plume meanders as it moves with the wind. At a smaller scale, patches with high odour concentrations are interspersed with regions where the concentration is very low. In this study, we address the behavioural decisions that individual fruit flies use in order to track a realistic odour plume towards a suitable resource. We model the odour distribution with a so-called filamentous plume that takes the features of a real odour plume into account. We constructed five individual-based models for odour-oriented flight patterns of *Drosophila melanogaster*, to investigate the effect of different sets of behavioural decision rules on the ability to find - and distinguish between – different odour sources that vary in suitability for reproduction. We compare the number of fruit flies that arrive at the odour sources for the five models based on different behavioural decisions with experimental data. Starting point for our individual-based model for fruit fly movement was an individual-based model for sex-pheromone oriented flight of male moths, that we parameterized for *D. melanogaster*. We found that behavioural decisions of moths could be used for odour tracking of fruit flies in a filamentous odour plume. However, these rules only were not sufficient to guide the fruit flies to the most suitable odour source. Fruit flies need to have a preference for the presence of food odours together with aggregation pheromone, over the presence of food odours in absence of aggregation pheromone, to be able to distinguish between odour sources. However, this stronger preference does not have to be fixed. As long as fruit flies are able to remember and adjust their current preference of “F+A” over “F” based on the odour concentrations of food odours and aggregation pheromone that they perceive, more fruit flies find the more attractive odour source. Furthermore, this study shows that including downwind flight when a fruit fly loses contact with the odour plume, and does not find the plume back again within 3 casts greatly enhanced the number of fruit flies that found the “F+A” odour sources.

Key words filamentous plume · individual-based model · arrival · odour source discrimination

6.1 Introduction

Many organisms use chemical cues to gather information about their environment, for instance about the presence of food, potential mates, suitable hosts, or natural enemies. These chemical cues are termed infochemicals (Dicke and Sabelis, 1988). Volatile infochemicals are distributed into the environment as the wind disperses odour molecules from their source, to form complex odour plumes. The main mechanisms of the distribution of odour are advection and turbulent diffusion. Advection transports the odour in the wind direction. Local and temporal variation of the wind direction causes the plume to meander. Turbulence stretches and stirs the odour puffs, and thereby creates odour-free gaps within the plume. This results in odour plumes with a complex spatial structure that varies with time.

The principal navigational mechanism used by flying insects to locate an odour source is to head upwind while in contact with the odour (Cardé, 1984; Murlis et al., 1992; Vickers, 2000). Insects use visual cues to control the ground speed in such a way that they move upwind (Frye et al., 2003). The movement of male moths in female-emitted pheromone plumes has been studied in detail (reviewed in Cardé and Mafra-Neto, 1997; Bakers and Vickers, 1997). From this is clear that moths that track a pheromone plume do not always fly directly upwind. When they lose contact with the plume they start casting, i.e. zigzagging – making regular turns, interspersed with wide lateral displacement roughly perpendicular to the wind direction. This kind of behaviour is also seen in fruit flies that track an odour plume in the air, when searching for food or an oviposition site (Kellogg et al., 1962; Frye et al., 2003; Budick and Dickinson, 2006).

How individual insects respond to odours and navigate in an odour plume has been studied in detail. However, to our knowledge, this is the first model study that addresses the behavioural decisions that are important for individuals to distinguish between different odours that are present in the environment and that indicate a difference in the quality of the odour source. We take the fruit fly *D. melanogaster* as a model organism. *Drosophila* fruit flies breed in ephemeral substrates, such as fermenting fruits, decaying plants, mushrooms or sap fluxes (Janssen et al., 1988). In *D. melanogaster*, attraction towards a blend of fermentation products from the food source, and towards its own aggregation pheromone (cis-vaccenyl acetate) plays a directive role in the aggregation on these resources (Hutner et al., 1937; Bartelt et al., 1985; Wertheim et al., 2006).

In this paper, we use individual-based models to study the effects of different behavioural responses of *D. melanogaster* on their ability to track an odour plume and to arrive at the odour source that is most suitable for reproduction. Our main question is which behaviours influence the ability of a fruit fly to trace an odour plume and to discriminate between suitable and less suitable odour sources. Our goal is to identify the combination of behavioural responses that gives the most realistic prediction of the spatial distribution of a fruit fly population when they can respond to multiple odour sources. Therefore, we modelled a realistic odour plume with respect to intermittency and meandering (after Farrell et al., 2002), and developed five individual-based models for fruit fly movement in such odour plumes. We compare the outcomes of the models with experimental data of Wertheim et al. (2002a).

6.2 Description of the model

Our aim is to investigate how behavioural decisions may be used by a fruit fly for tracking a realistic odour plume (Farrell et al., 2002) and for distinguishing between odours from suitable and less suitable resources for reproduction. For this purpose, we developed five individual-based models (IBMs) with increasing behavioural complexity. We start with a basic model based on odour-plume tracking by moths (Yamanaka et al., 2003) and in a stepwise manner we add specific features of fruit fly navigation in odour plumes that have been observed for free-flying fruit flies in an experimental set-up (Kellogg et al., 1962; Frye et al., 2003; Budick and Dickinson, 2006). The main variables in the model are the concentration of (1) food odours ($F(x, y, t)$) and of (2) the aggregation pheromone of *D. melanogaster* ($A(x, y, t)$), and (3) the position of the individual fruit flies ($N(x, y, t)$). As we are interested in the behavioural decisions in a realistic odour plume, we focus on the short-term and simulate the arrival of the fruit flies at the odour sources for 30 minutes. In the experiments of Wertheim et al. (2002a) fruit fly arrival tended to increase up to 30 minutes and then levelled off.

6.2.1 Odour distribution – filamentous plume model

For the odour distribution we adopt a plume model developed by Farrell et al (2002) that mimics the intermittency and meandering characteristics of a real odour plume: the centre line of the odour plume meanders and the odour plume has an intermittent internal structure, where parts with high odour concentrations are interspersed with spots without odour molecules. In this model, the plume consists of spherically shaped odour filaments with an instantaneously changing odour concentration. The velocity vector of an odour particle consists of three components: (I) the transport of the plume as a whole (advection and turbulence) (Eqs. 3-4), (II) the transport within the body of the plume (diffusion relative to the centre line), and (III) the expansion of the filament (Eqn. 6).

The transport of the plume as a whole is modelled by,

$$\frac{\partial \overline{u}}{\partial t} = -\overline{u}\frac{\partial \overline{u}}{\partial x} - \overline{v}\frac{\partial \overline{u}}{\partial y} + \frac{1}{2}K_x\frac{\partial^2 \overline{u}}{\partial x^2} + \frac{1}{2}K_y\frac{\partial^2 \overline{u}}{\partial y^2}, \tag{3}$$

$$\frac{\partial \overline{v}}{\partial t} = -\overline{u}\frac{\partial \overline{v}}{\partial x} - \overline{v}\frac{\partial \overline{v}}{\partial y} + \frac{1}{2}K_x\frac{\partial^2 \overline{v}}{\partial x^2} + \frac{1}{2}K_y\frac{\partial^2 \overline{v}}{\partial y^2}, \tag{4}$$

where $\overline{u}$ and $\overline{v}$ are the mean velocities of a turbulent flow, in respectively the x and y direction, and K_x and K_y represent the diffusivity in the longitudinal and transversal direction. These equations were solved numerically. We use red noise to ensure that the spatial and temporal correlation in wind speed and wind direction is high. The red noise process at each corner of the domain is implemented by filtering Gaussian white noise with the transfer function

$$H(s) = G\frac{a}{s^2 + bs + a}. \tag{5}$$

The boundary condition along the edge nodes is generated by interpolating between the values of the two adjacent corners. Implementation of this model for advection yields a continuous, spatio-temporally varying wind field. We ran our simulations with (a, b, G)=(0.06 rad^2 s^{-2}, 0.1 rad s^{-1}, 4). This generated a small amplitude meander.

The diffusion relative to the centre line is implemented as a white noise process with spectral density σ_v.

The expansion of the filament is modelled by

$$R_i^2(t) = R_i^2(0) + \gamma t, \tag{6}$$

where R_i is the radius of the i-th filament. At the time of release of the filament the radius $R_i(0) = \sqrt{0.001}$ m. The growth rate of the filament is $\gamma = 0.001$ m^2 s^{-1}.

In our simulations, we evaluate the odour concentration at point (x, y) in the domain by determining which filaments are present at that point and by calculating the odour distribution within the filaments as

$$I_i(x,y,t) = \frac{Q}{2\pi R_i^2(t)} \exp\left(-\frac{(x - x_i) + (y - y_i)}{2R_i^2(t)} \right), \tag{7}$$

where $I_i(x, y, t)$ is the instantaneous odour concentration at point (x, y) at time t due to the i-th filament, and (x_i, y_i) is the centre of the i-th filament. The amount of odour in one filament, Q, is the odour production by the odour source (either only food odours θ_F, or food odours θ_F and aggregation pheromone θ_A) per second divided by the number of filaments released per second, ψ. The overall instantaneous odour concentration at point (x, y) is calculated as the sum of the concentrations of the filaments that are present at that location:

$$I(x,y,t) = \sum_{m=1}^{M} \sum_{i=1}^{N_m} I_i(x,y,t), \tag{8}$$

where M is the number of odour sources in the simulation, and N_m is the number of filaments currently in the simulation that originated from source m.

6.2.2 Movement of fruit flies

We constructed five individual-based models (IBMs) for odour-oriented flight of searching fruit flies to analyse which behavioural decision rules are important to track an odour plume and distinguish between odour sources that differ in attractiveness. All five models have the same kernel, but in a stepwise manner we add new behavioural rules. For a description of the parameters and their default values we refer to Table 1.

The basic model

The starting point for modelling the fruit fly motion is an individual-based model developed for sex-pheromone oriented flight of male moths (Yamanaka et al., 2003), that we parameterized for *D. melanogaster* (Budick and Dickinson, 2006). Our basic model includes three types of flight patterns: random flight, upwind flight, and zigzag flight. When a fruit fly detects an odour plume, it starts upwind flight guided by anemotaxis. The instantaneous wind direction only infrequently aims at the odour source. Therefore, just simply heading upwind while in the plume not necessarily leads the fruit fly towards the source of the odour. Upwind flight often carries an insect out of the meandering plume. When it loses the plume, it makes a crosswind turn. This type of turning, known as zigzag flight, enhances the likelihood of re-encountering the odour plume. If it does not re-encounter the odour plume within a certain amount of zigzags, the fruit fly resumes random flight.

In each simulation of 30 minutes, all fruit flies start with random flight until they encounter an odour filament. The distance covered during the random flight in one time step (relative to the surrounding air) is drawn from a Gaussian distribution, with mean: μ_r and SD: σ_r. The change in direction (relative to the surrounding air) is also drawn from a Gaussian distribution, with mean: 0° and SD: σ_rdeg. The resulting trajectory in the 2-D plane depends on the velocity and direction of the random flight and the velocity and direction of the instantaneous wind. When a fruit fly encounters an odour filament it instantly stops its random flight and starts the upwind flight. It flies with a constant speed (relative to the surrounding air): c_{up} and directed against the instantaneous wind direction. The net distance upwind (relative to the ground) depends on the instantaneous wind speed. We assume that a fruit fly encounters an odour filament when the value of its sensory index $f(F,A)$ (see below) is greater than a threshold value f_t. If the fly still detects an odour filament in the next time step, it continues flying upwind. If no odour is detected in the next time step, the fly starts the zigzag flight. The distance covered in the zigzag flight in one time step is drawn from a Gaussian distribution, with mean: μ_{zz} and SD: σ_{zz}. The fruit fly flies across the local wind direction. The fruit fly performs the zigzag flight over several time steps. If the fruit fly does not re-encounter an odour filament within max_{zz} time steps, the fruit fly resumes random flight. If a fruit fly flies above an odour source (a circle with 5 cm radius), it arrives at the odour source. After having arrived, it stays on the resource for the remaining simulation time.

The incentive model

Bartelt et al. (1985) showed for the response of *D. melanogaster* towards its aggregation pheromone and food odours, that (1) *D. melanogaster* is about four times more attracted to the combination of its aggregation pheromone and food odours, than to food odours alone, but that (2) the aggregation pheromone is only attractive when food odours are also present. A description of the response of *D. melanogaster* to infochemicals that is consistent with these findings (see Lof et al., 2008; **Chapter 2**) is supplied by the sensory index function

$$f(F,A) = \frac{F}{F_0 + F} + \eta \frac{FA}{F_0 A_0 + FA}. \tag{11}$$

The incentive model is an expansion of the basic model. Fruit flies still exhibit three types of flight patterns: random flight, upwind flight, and zigzag flight (Fig. 1). However, a fruit fly in our incentive model has a preference for higher values for the sensory-index function. When a fruit fly loses contact with an odour plume that consisted of both food odours and aggregation pheromone during upwind flight it has a high expectation level f_i. If it finds, by zigzag flight, an odour plume that consists of only food odours, its expectation is not met, and it rejects the plume and continues zigzagging. The fruit fly stops zigzagging either when it again finds an odour plume for which the response value exceeds its current expectation level, after which it starts upwind flight, or when it reaches the maximum number of zigzag casts (max_{zz}), after which it starts searching randomly. The value of its expectation level f_i varies over time. While the fruit fly flies upwind, f_i increases if it perceives a higher value of its sensory-index function. If no higher value is perceived, f_i decays over time with, $f_i(t+1) = \omega f_i(t)$ with $\omega<1$.

In a filamentous odour plume there are many local optima in odour concentration (i.e. each odour filament in the plume has its own local optimum). In such a local optimum, its expectation level may accidentally be higher than the value of its sensory index function in the upwind direction, although that still may be within the plume. In that case, it would erroneously start to zigzag and probably lose contact with the plume. To prevent this kind of mishap, the fruit flies continue flying upwind when the value for the sensory-index $f(F,A)$ is larger than or equal to than $\delta * f_i$, with $\delta<1$. In this way, the behaviour becomes less sensitive to the actual value of f_i. Finally, the threshold value for response to odours f_t in the basic model is implemented as a minimum value for f_i of f_t/δ. In summary, in each time step the expectation level f_i is calculated as the maximum of three values,

$f_i(t) = max(f(F,A), \omega f_i(t - \Delta t), (1/\delta) f_t)$

An incentive is an external motivation that induces action. Our incentive model simulates the situation where there is no innate preference for the presence of aggregation pheromones. In this set-up, when a fruit fly starts in the plume that only contains food odours it tracks this plume towards the odour source, unless it loses contact with this plume and finds the food odour plus aggregation pheromone plume; then it is stimulated to fly upwind only if the odour plume also contains aggregation pheromone.

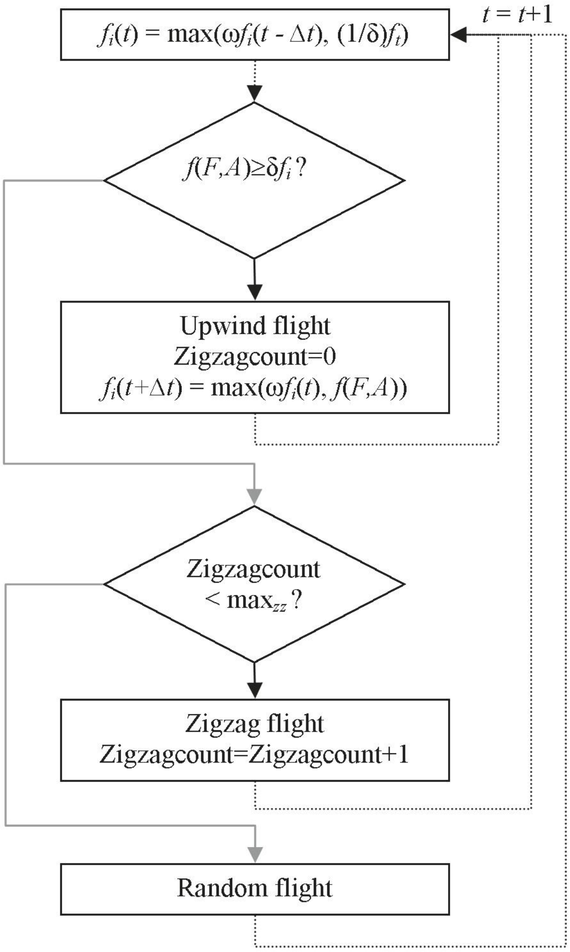


Figure 1 Schematic representation of the behavioural decisions made during fruit fly movement. In our simulations each fruit fly starts in random flight until it encounters it first odour filament with a value of its sensory index $f(F,A)$ greater than a threshold value f_t. Every time step starts with updating the current threshold value for the sensory index $f_i(t)$ (except for the basic model, because this has a fixed threshold value f_t). Black arrows denote a condition that is met. Grey arrows denote conditions that are not met. Dotted arrows going up represent the end of a time step.

The motivation model

The motivation model is a special case of the incentive model. We assume that for the fruit fly to start to fly upwind, it is necessary that aggregation pheromone is present (i.e. it has an internal preference), that is, the flies will not respond to food odours alone. As the term $F/(F_0+F)$ in (11) has a maximum value of 1, this behaviour can be accomplished in the model by adopting a threshold value f_t of at least $1/\delta$ (to take into account the insensitivity of the fruit fly to the actual value of its preference f_m). This is a stronger preference than the actual preference of *D. melanogaster*.

The vision model

The vision model is an expansion of the incentive model. In the vision model, a fruit fly flies randomly, flies upwind or performs zigzag flight, as in the models above. To continue flying upwind, a fruit fly should perceive a value for the sensory-index $f(F,A)$ equal to or higher than the current value of $\delta * f_i$. However, in the vision model the fruit fly not only uses olfactory cues to find the odour source but also adjusts its behaviour when it is close enough to the odour source to be able to see it. Frye et al. (2003) found that *D. melanogaster* reduced crosswind cast length when it was close to an odour source. Based on their work, we reduced the distance of the zigzag flight in one time step by a fraction $\xi=0.3$ within a radius $r=0.1$ m from the odour source. In this area, the mean zigzag speed is: $(1-\xi)\mu_{zz}$, the standard deviation remains the same: σ_{zz}. In the vision model the zigzag speed is only affected when the fruit fly is in the proximity of the odour source while the direction of the flight is unaltered.

Table 1 Description and values of parameters used in simulations

Parameter	Description	Value	unit
Δt	Integration step of the wind velocity field	0.01	s
$\bar{u}$	Mean velocity advection infochemicals in x-direction	0.35	m s^{-1}
$\bar{v}$	Mean velocity advection infochemicals in y-direction	0	m s^{-1}
K_x, K_y	Diffusivity of the filamentous odour plume	1^{b}	$m^2 s^{-1}$
σ_v^2	Power spectral density centerline relative diffusion filamentous plume	4^{b}	$m^2 s^{-1}$
$R(0)$	Filament radius at time of release	$\sqrt{0.001}$ ^{b}	m
γ	Filament growth rate	0.001^{b}	$m^2 s^{-1}$
θ_F	Food odour production by the odour source	42.64^{c}	ng $s^{-1} m^{-2}$
θ_A	Aggregation pheromone production by the odour source	8.74^{c}	ng $s^{-1} m^{-2}$
Ψ	Number of filaments released per second	50	s^{-1}
Δt_{Dm}	Time step of fruit fly movement	0.1	s
μ_r	Mean velocity during random flight	0.55^{d}	m s^{-1}
σ_r	Standard deviation of mean velocity of random flight	0.11^{d}	
μ_{rdeg}	Mean heading of random flight	0^{e}	^{o}
σ_{rdeg}	Standard deviation of mean heading of random flight	45^{e}	
c_{up}	Velocity during upwind flight	0.59^{d}	m s^{-1}
μ_{zz}	Mean velocity during zigzag flight	0.25^{d}	m s^{-1}
σ_{zz}	Standard deviation of mean velocity of zigzag flight	0.05^{d}	
max_{zz}	Maximum number of zigzag casts	25^{f}	-
Ξ	Fraction of zigzag speed reduction close to odour source	0.3^{g}	-
R	Radius around odour source where zigzag speed is reduced	0.075^{g}	m
μ_{dw}	Mean downwind displacement during downwind flight	0.375^{h}	m
σ_{dw}	Standard deviation of mean downwind displacement	0.1^{h}	
F_0	Saturation parameter for food odours	10^{c}	ng m^{-2}
A_0	Saturation parameter for aggregation pheromones	0.04^{c}	ng m^{-2}
H	A measure for the attraction of food odours combined with aggregation pheromone relative to the attraction to food odours alone.	1.5	
f_t	Minimum value of the sensory index $f(F,A)$ above which fruit flies start to respond to odours	0.1	ng m^{-2}
ω	Decay of the expectation level f_i per time step Δt	0.99	
δ	Insensitivity for actual value of the variable expectation level f_i above which fruit flies start to respond to odours	0.8	

[a] Lof et al., 2007, [b] Farrell et al., 2002, [c] de Gee et al., 2008, [d] Budick and Dickinson, 2006, [e] Yamanaka et al., 2003, [f] $max_{zz}=25$ for the basic, the incentive, the motivation and the vision model, for the downwind model $max_{zz}=3$, [g] Frye et al., 2003, [h] Kellogg et al., 1962.

Table 2 Summary of the distinctive features of the five individual-based models for fruit fly behaviour during odour plume tracking.

			Model type		
	Basic	**Incentive**	**Motivation**	**Vision**	**Downwind**
Flight types	1. Random 2. Upwind 3. Zigzag	1. Random 2. Upwind 3. Zigzag	1. Random 2. Upwind 3. Zigzag	1. Random 2. Upwind 3. Zigzag	1. Random 2. Upwind 3. Zigzag 4. Downwind
Threshold value for upwind flight f_t	0.1	0.1	1.25	0.1	0.1
Expectation level f_i	Fixed at f_t	$f_i(t) = max(f(F,A), 0.99*f_i(t-\Delta t), 1.25f_t)$	$f_i(t) = max(f(F,A), 0.99*f_i(t-\Delta t), 1.25f_t)$	$f_i(t) = max(f(F,A), 0.99*f_i(t-\Delta t), 1.25f_t)$	$f_i(t) = max(f(F,A), 0.99*f_i(t-\Delta t), 1.25f_t)$
Maximum number of zigzag casts	25	25	25	25	3
Special rules	-	-	-	Length of zig zag cast is reduced with 70%, within 0.1m distance from patch edge.	If zig zag count = max_{zz}, downwind flight. If not encountered plume resume zigzag flight.

The downwind model

Kellogg et al. (1962) found that the cross-wind casts of *D. melanogaster* usually last about 0.3 seconds. Therefore, in this model the maximum number of zigzag casts is reduced to 3. If the fruit fly fails to re-encounter the odour plume during these 3 zigzag casts, it flies downwind for a distance of 0.15 to 0.6 m, before resuming the zigzag flight. For this model, the distance of the net downwind flight in one time step is drawn from a Gaussian distribution with mean: μ_{dw} and SD: σ_{dw}. These are net downwind distances. The fruit fly moves downwind with the instantaneous wind direction. The downwind model is an expansion of the incentive model.

The distinctive features of the above five individual-based models are summarised in table 2.

6.2.3 Simulation set-up

We used the parameter values as given in Table 1. We considered a spatial domain of 30 m × 30 m, with the lower left corner $(x, y) = (0, 0)$. We used absorbing boundaries for the odour distribution, so odours can diffuse out of the spatial domain. We compare our simulation results with the experiments of Wertheim et al. (2002a) (see paragraph 2.4). These experiments were conducted in a population cage from which the fruit flies could not leave. Therefore, in our simulations fruit flies also cannot leave the domain. We model this by using reflecting boundaries. Odour dispersal was simulated with time steps of 0.01 second, and movement of the fruit flies was simulated with time steps of 0.1 second. Per second, each odour source released 50 odour filaments. In each simulation, 400 fruit flies were released at the point (x, y) = (9, 15). This release point is situated one meter downwind from the nearest odour source, and centred between the two (rows of) odour sources.

In our simulations, we considered two or eight odour sources that continuously emit infochemicals. We used two types of odour sources. The first source type, “F+A”, emits food odours together with the aggregation pheromone. The presence of this combination of odours indicates that the source is highly suitable for reproduction because there is a food source and other fruit flies are or have been present. The second odour source type (for less suitable resources), “F”, emits food odours alone. The presence of food odours without aggregation pheromone indicates that the source is potentially suitable for reproduction, but that no other fruit flies have been present (yet).

We used two simulation set-ups to compare fruit fly arrival for the five individual-based models. In the first set-up, we compared the arrival of the fruit flies on two odour sources (“R2”), placed one meter apart, situated five meter upwind from the initial fruit fly population. One of the odour sources contained only food odours (“F”) and the other contained both food odours and aggregation pheromone (“F+A”). We used these simulations to compare the ability of fruit flies to distinguish between the two types of odour sources. We ran the simulation for 10 minutes and recorded the fruit fly arrival. Both the filamentous plume sub-model and the individual-based sub-models are stochastic. Therefore, we ran the simulations 10 times to verify the consistency of the results.

In the second setup, we compared the arrival of the fruit flies on eight odour sources (“R8”). In this set-up, four odour sources containing only food odours and four odour sources containing food odours and aggregation pheromone were placed in two rows one meter apart, F and F+A sources alternating (one meter apart) (Fig. 2). The sources were placed in the centre of the field in y-direction (y = 14.5 or 15.5 m) and upwind in the x-direction (x = 5, 6, 7 or 8 m). We ran the simulation for 30 minutes and recorded the number of fruit flies that arrived. We again ran the simulations 10 times to verify the consistency of the results.

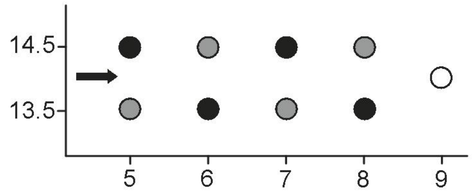


Figure 2 Spatial set-up of the simulations with eight odour sources. Black dots mark the “F+A” odour sources, dark grey dots mark the “F” odour sources. The white dot marks the fruit fly release point. The black arrow depicts the average wind direction. The x-axis and y-axis give the position of the odour sources in the grid given in meters from the lower left corner.

6.2.4 Model validation

To evaluate which of the five individual-based models for fruit fly movement in odour plumes generates the most realistic results, we compared our simulation results for a situation with two odour sources “R2” and one with eight odour source “R8” with the outcome of an experimental study by Wertheim et al. (2002a). That study addressed the behavioural responses of *D. melanogaster* to pheromone-treated and control substrates in an outdoor population cage. In this cage, they positioned eight substrates: four control substrates and four pheromone-treated substrates in two rows, treatment and control substrates alternating. This experiment was repeated on three days. The spatial set-up in our R8 simulations was designed after this experiment. To enable a comparison with the data of Wertheim et al. (2002a), we based the pheromone production in our simulations on the pheromone concentration used in this experiment. A large part of the 800 fruit flies remained in the release container during the first hour of the experiment (Wertheim et al., 2002a). Therefore, we assumed in our simulations that in the first 30 minutes of the experiment 400 fruit flies started dispersing.

Fruit fly arrival at two odour sources ("R2")

For comparison of the experimental data with the "R2" set-up in the model, we used the experimental data on the total numbers arrived at all control substrates (emitting only food odours) after 10 minutes and considered this total arrival as the arrival at one "F" source. Furthermore, we used the experimental data on the total arrival at all pheromone-treated substrates (emitting both food odour and aggregation pheromone) after 10 minutes and considered this total number the arrival at one "F+A" source. Wertheim and co-workers did three replicates of this experiment. We compared the total arrival after 10 minutes on the control and the pheromone-treated substrates in the three replicates of the empirical experiment (Wertheim et al., 2002a) with the arrival after 10 minutes in the 10 replicates of our simulations on the "F" and the "F+A" source.

Fruit fly arrival at eight odour sources ("R8")

For comparison of the experimental data with the "R8" set-up in the model, we used the data on the total arrival at all control substrates (emitting only food odours) and the total arrival at all pheromone-treated substrates (emitting both food odour and aggregation pheromone) after the first 30 minutes of the field experiment of Wertheim et al. (2002a). We compared the numbers arrived in 10 replicates from our simulations with the numbers arrived at the control and the pheromone-treated substrates in the three replicates of the empirical experiment.

Furthermore, we looked at the spatial distribution of the numbers arrived. Therefore, we compared the number arrived in the simulations per resource with the experimental numbers arrived at the substrates with the same treatment and the same spatial position relative to the release point in the field-experiment of Wertheim et al. (2002a).

6.2.5 Statistics

Data analysis for fruit fly arrival at two odour emitting patches ("R2")

We used a logistic regression model to analyse the fraction of fruit flies that arrived at the "F+A" and "F" patches together. Given that the fruit flies arrived on one of the two patches, we also analysed the fraction of the arrived fruit flies that arrived at the "F+A" patch. To account for extra-binomial variation (or overdispersion) that was present in our data, we used an extra scale parameter. We used Wald-tests to compare the fractions of the fruit flies that arrive in total or that arrive on the "F+A" patch of all five different simulation models with fractions of arrival found in the field experiment by Wertheim et al. (2002a).

Data analysis for fruit fly arrival at eight odour emitting patches ("R8")

We used a logistic regression model accounting for overdispersion to analyse the fraction arrived at the eight odour-emitting patches together. We compared the fractions of the fruit flies that arrive in total or that arrive on the "F+A" patch for the different simulation models to the fractions of arrival found in the field experiment by Wertheim et al., 2002a.

The spatial distribution of the arriving fruit flies was analysed using three-way weighted ANOVA, with interaction. We analysed the arcsine square root transformation of the fraction of fruit flies arriving at each patch. The number of fruit flies arriving at any of the eight patches was used as weight. The three factors, explaining the mean fraction arriving at a patch, were (a) distance from the release site (four levels), (b) absence/presence of the aggregation pheromone, and (c) data source (real data or simulated model based data). We compared each of the five models with the experimental data from the field experiment by Wertheim et al. (2002a).

6.3 Results

6.3.1 Fruit fly arrival at two odour emitting patches ("R2")

In the field experiment of Wertheim et al. (2002a) on average a total of 124 (±85) fruit flies arrived at the eight "F+A" and "F" patches. The mean fraction of arriving fruit flies at all patches was 0.31 (SD=0.21). The mean fractions of arriving fruit flies at the two patches "F+A" and "F" together after 10 minutes of dispersal were not significantly different from the mean fraction from the data for the basic (χ^2= 0.33, P= 0.56), the incentive (χ^2= 0.23, P=0.63), the motivation (χ^2= 1.63, P=0.20) and the vision model (χ^2= 0.26, P=0.61) (Table 3). The downwind model was significantly different from the data: after 10 minutes the mean fraction of arriving fruit flies at both patches was 0.741 (χ^2= 6.37, P=0.012).

The mean fraction of fruit flies that arrived at the source that emitted both food odours and aggregation pheromone "F+A" was for the basic model 0.378 (χ^2=5.23, P=0.022) and for the downwind model 0.996 (χ^2=4.66, P=0.031) (Table 3). Both values were significantly different from the fraction experimentally found in the field experiment of Wertheim et al. (2002a). The fraction of fruit flies that arrived at the "F+A" patch for the incentive (χ^2=0.0, P=1), motivation (χ^2=1.03, P=0.31) and vision (χ^2=0.38, P=0.54) model were not significantly different from the fraction experimentally found in the field experiment of Wertheim et al. (2002a).

6.3.2 Fruit fly arrival at eight odour sources ("R8")

In the field experiment of Wertheim et al. (2002a) on average a total of 133 (± 11) fruit flies arrived at the four "F+A" sources and on average a total of 37(±9) fruit flies arrived at the four "F" sources in the first 30 minutes of the experiment (Fig. 3).

Table 3 Fraction of the initial 400 fruit flies that arrive at the "F+A" and the "F" source together, and fraction of all arrived fruit flies that arrived at the "F+A" source only, for the basic, the incentive, the motivation, the vision and the downwind model after 10 minutes of the "R2" simulation over 10 replicates. Field data refers to 3 replicates of the field experiment of Wertheim et al. (2002a). The 95% confidence interval of the estimated mean is given in the column "Range".

	Fruit fly arrival at "F+A" and "F"		**Fruit fly arrival at "F+A"**	
	Mean fraction of total	Range	Mean fraction of arrived	Range
Field data	0.309	0.114 – 0.609	0.822	0.495 – 0.956
Basic	0.226	0.121 – 0.383	0.378	0.218 – 0.571
Incentive	0.238	0.130 – 0.396	0.822	0.637 – 0.924
Motivation	0.141	0.062 – 0.289	0.639	0.394 – 0.829
Vision	0.235	0.127 – 0.393	0.896	0.717 – 0.967
Downwind	0.741	0.582 – 0.854	0.996	0.905 – 1.000

Table 4 Mean fraction of the initial 400 fruit flies that arrive at all "F+A" and "F" sources together, and fraction of all arrived fruit flies that arrived at the "F+A" sources only, for the basic, incentive, motivation and downwind model after 30 minutes of the "R8" simulation over 10 replicates. Field data refers to 3 replicates of the field experiment of Wertheim et al. (2002a). The 95% confidence interval of the estimated mean is given in the column "Range".

	Fruit fly arrival at "F+A" and "F"		**Fruit fly arrival at "F+A"**	
	Mean fraction of total	Range	Mean fraction of arrived	Range
Field data	0.426	0.244 – 0.630	0.781	0.599 – 0.895
Basic	0.185	0.113 – 0.289	0.332	0.209 – 0.484
Incentive	0.320	0.225 – 0.433	0.843	0.742 – 0.909
Motivation	0.135	0.075 – 0.232	0.729	0.551 – 0.855
Vision	0.231	0.149 – 0.339	0.827	0.702 – 0.906
Downwind	0.998	0.792 – 1.000	0.999	0.924 – 1.000

Table 5 Mean fraction of the fruit flies that arrived at a particular distance given for the eight odour sources (one to four meter from the release point) for the basic, the incentive, the motivation, the vision and the downwind model after 30 minutes of the "R8" simulation over 10 replicates. Field data refers to data from the field experiment of Wertheim et al. (2002a).

	1m		**2m**		**3m**		**4m**	
	"F+A"	**"F"**	**"F+A"**	**"F"**	**"F+A"**	**"F"**	**"F+A"**	**"F"**
Field data	0.264	0.086	0.221	0.063	0.149	0.057	0.147	0.014
Basic	0.011	0.003	0.011	0.001	0.036	0.005	0.274	0.659
Incentive	0.004	0.001	0	0.002	0.050	0.002	0.789	0.152
Motivation	0.009	0.002	0	0.004	0.232	0.004	0.488	0.262
Vision	0	0	0.001	0.002	0.168	0.002	0.658	0.169
Downwind	0	0	0	0	0.027	0.001	0.972	0

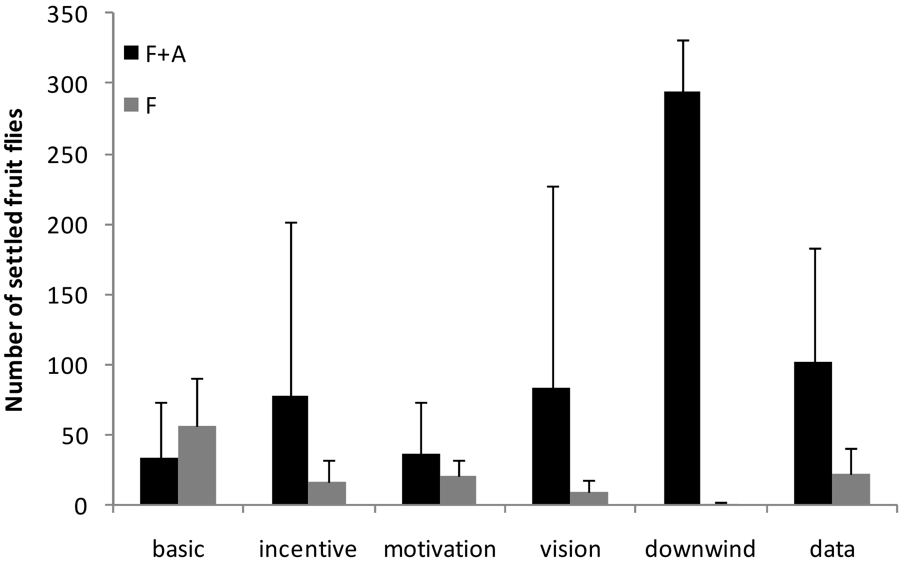


Figure 3 Average numbers of fruit flies that arrived at the "F+A" sources (black bars) and "F" sources (gray bars) for the basic, incentive, motivation, vision and downwind model after 10 minutes of the "*R2*" simulation for 10 replicates. The bars at the far right depict data from the field experiment of Wertheim et al. (2002a). These bars depict the total number of fruit flies arrived at the four "F+A" or the four "F" sources after 10 minutes, averaged over three replicates of the field experiment. Error bars depict one standard deviation.

The mean fraction of the total number of fruit flies in the experiment that arrives at a patch was 0.426 (Table 4). Of the fruit flies that arrived at a patch 78.1% of the fruit flies arrived at one of the “F+A” patches. The mean fraction of the initial number of 400 fruit flies arriving at any patch was significantly different from the data for the basic (χ^2= 5.22, P=0.022), the motivation (χ^2= 8.30, P=0.004) and the downwind (χ^2= 6.74, P=0.01) model. The fruit flies in the basic model were not able to discriminate between the two odour sources. On average, more fruit flies arrived at an “F” patch than at an “F+A” patch (Table 4). In all other models, fruit flies predominantly arrived at an “F+A” patch. The mean fraction of arriving fruit flies at all “F+A” and “F” patches together after 30 minutes of dispersal were not significantly different from the mean fraction from the data for the incentive (χ^2= 0.86, P=0.35) and the vision (χ^2= 3.22, P=0.073) model.

Consistent to what was found in the simulations with two odour patches, the mean fraction of fruit flies that arrived at the sources that emitted both food odours and aggregation pheromone “F+A” were significantly different from the fractions found in the experimental data for the basic model (χ^2=12.89, P<0.001) and for the downwind model (χ^2=5.92, P=0.015) (Table 3). The fraction of fruit flies that arrived at the “F+A” patches for the incentive (χ^2=0.56, P=0.45), motivation (χ^2=0.22, P=0.64) and vision (χ^2=0.26, P=0.61) model were not significantly different from the fraction experimentally found in the field experiment of Wertheim et al. (2002a).

Spatial distribution (“R8”)

In the field experiment (Wertheim et al., 2002a), the sources closest to the release point of the fruit flies were found first. Most fruit flies arrived at these odour sources. The fraction of fruit flies that arrived at an odour source decreased with distance from the release point. In our simulations we found the opposite: the odour sources that were furthest away from the release point attracted most fruit flies (Table 5). In all five individual-based models, less than 2% of the fruit flies that arrived at a patch during the 30 simulation minutes, arrived at the 4 odour sources (both “F+A” and “F”) closest to the release point. A slightly higher fraction of fruit flies arrived at the “F+A” odour source three meter upwind from the release point. In the incentive, the vision and the downwind model fruit flies predominantly arrived at the “F+A” source 4 meter upwind from the release point of the fruit flies; “F+A” (Table 5). While, in the basic model, on average more fruit flies arrived at the “F” source four meter upwind from the release point. Using three-way weighted ANOVA, with interaction (see §2.5.2) we showed that the spatial distribution of the arriving fruit flies was significantly different from the data for all 5 studied individual-based models (basic: $F_{7,63}$=41.46, incentive: $F_{7,63}$=15.66, motivation: $F_{7,63}$=19.13, vision: $F_{7,63}$=12.38, downwind: $F_{7,63}$=88.75, all P<0.0001).

6.4 Discussion

If we only look at the fraction of arriving fruit flies in the simulations, the incentive model, and the vision model match the results from the field experiment best. The motivation model underestimates the number of fruit flies that arrive at a patch (Table 4). The basic model underestimates the number of fruit flies that arrive at the “F+A” source. While, the downwind model overestimates the number of fruit flies that arrive at the “F+A” source, and underestimates the arrival at the “F” source. In the field experiment by Wertheim et al. (2002a) the fraction of fruit flies that arrived at an odour source decreased with distance from the release point. In our simulations we found the opposite: the odour sources that were furthest away from the release point attracted the most fruit flies (Table 5). The models were not able to predict the spatial distribution of the arrivals correctly.

All models show significant differences in mean (transformed) fractions, compared to the real data. Within the set of models currently developed, the incentive and the vision model, show the smallest deviation from the real data. In every model tested, the number of fruit flies that arrived at the patch that emitted both food odours and aggregation pheromone “F+A” was more variable than the number of fruit flies that arrived at the “F” patch (Fig. 3). This variability was the highest in the incentive and the vision model, where the fruit fly’s preference to fly towards a specific odour source depended on the first odour filament that it encountered. If the first odour contact was in an “F+A” plume it preferred to stay in that plume to find that odour source. If the first odour contact was in an “F” plume, it would start tracking this plume to its source. Only if it lost track of this plume, it had the chance to find the “F+A” plume and trace this. Remarkably, also in the motivation model – where fruit flies had an innate preference for the presence of aggregation pheromone, which was set such that the “F” plume could not be sensed by the fruit fly – a third of the fruit flies that arrived at a patch arrived at the “F” patch by chance. Our model is in 2D; therefore, if the fruit fly is above an odour source it arrived at that odour source, while in reality it flies over the source if that source does not emit the odour it is tracking

6.4.1 Towards modelling fruit fly movement in odour plumes

Our original idea was to compare a Gaussian plume and the filamentous plume (Farrell et al., 2002) in combination with the integro-difference model (IDE) for fruit fly distribution that we used in Chapters 2-5. Thus, we set out to study the spatial distribution of the fruit flies and their arrival at the odour sources when they can respond to one of the two odour plume models, and to compare which odour plume model could best describe the distribution of arrived fruit flies as found in the cage experiment by Wertheim et al. (2002a). Although, the IDE method for fruit fly dispersal works perfectly in combination with the Gaussian plume, as they both use time-averaged distribution patterns of fruit flies or odour concentrations respectively, it did not work for the filamentous plume model. The combination of an instantaneous odour plume model, with large variation of odour concentrations both in the temporal and the spatial scale (even with very small spatial and temporal steps) with the IDE method proved too problematic. We used various approaches to model population distributions in combination with the filamentous plume.

First we tried to use a finite difference method, where central differences were applied to the spatial variables to convert the partial differential equation (PDE) for chemotactic movement of the fruit fly population into a system of coupled ordinal differential equations (ODEs). We solved the resulting system of coupled differential equations by using the explicit Runge-Kutta 45 method of Dormand and Prince (1980) and we did a straightforward discretization. This resulted in a mass-conservative approximation of the dispersion (i.e. the number of fruit flies before and after the dispersion step were the same), but not in a mass-conservative approximation of the chemotaxis (i.e. the number of fruit flies after the chemotaxis step changed). This proved to be especially harmful in regions where the gradient of the sensory index function has large spatial variations. Then, we tried to do this in a mass-conservative way, i.e. without changing the number of fruit flies in the field. To make the chemotaxis mass-conservative, spatial differences were used not on the variable N_S (the searching fruit fly population), but on the flux of N_S:

$$\frac{\partial}{\partial t}N_{x,y} = D_P\left[\frac{N_{x+\Delta x,y} - 2N_{x,y} + N_{x-\Delta x,y}}{(\Delta x)^2} + \frac{N_{x,y+\Delta y} - 2N_{x,y} + N_{x,y-\Delta y}}{(\Delta y)^2}\right]$$
$$-\nu\left[\frac{\frac{N_{x+\Delta x,y} + N_{x,y}}{2}\,\frac{f_{x+\Delta x,y} - f_{x,y}}{\Delta x} - \frac{N_{x,y} + N_{x-\Delta x,y}}{2}\,\frac{f_{x,y} - f_{x-\Delta x,y}}{\Delta x}}{\Delta x}\right] \tag{12}$$
$$-\nu\left[\frac{\frac{N_{x,y+\Delta y} + N_{x,y}}{2}\,\frac{f_{x,y+\Delta y} - f_{x,y}}{\Delta y} - \frac{N_{x,y} + N_{x,y-\Delta y}}{2}\,\frac{f_{x,y} - f_{x,y-\Delta y}}{\Delta y}}{\Delta y}\right]$$

In this equation, $N_{i,j}$ denotes the density of the searching population in point i,j, $f_{i,j}$ denotes the population response to both aggregation pheromones and food odours at point i,j (calculated by Eq. 11), Δx and Δy are the spatial steps in x and y-direction respectively, D_N is the diffusion constant of the fruit fly population and ν denotes the strength of the chemical attraction (the latter parameter is not used in our IBM's). Again, we used the Runge-Kutta 45 method to solve the system of coupled differential equations. However, even by including the flux of N_S in the chemotaxis we could not make the calculations conservative in the number of fruit flies in the field.

Next, we used the original IDE method again, but now increased the number of terms in our truncated series approximation (Powell et al., 1998, see Eqn. A.7 in Chapter 5). However, this did not improve the stability of the model. In the IDE method, the calculation of the new population distribution involved a normalization step and due to very large variation of odour concentrations on very small spatial and temporal scales this normalization step introduced large errors. A reduction in the time steps used in the IDE model prevented the fruit flies to move because the spatial step they could make in one time step was smaller than the spatial resolution of the grid cells. Moreover, the advantage of using the IDE approach over other numerical approaches is that it can use large time steps to approximate the spatial distribution and therefore can calculate population distributions faster than other numerical approaches (Powell et al., 1998). By using a very small time step, the IDE approach loses the advantage of faster calculations and it increases its error, because a larger number of approximations are needed to calculate the population distribution.

The final attempt to model population distributions was a numerical approach where we used the built-in ode23s solver from Matlab, which is especially suitable for stiff systems. It is more stable, but with a lower accuracy. Also with this method, we had problems with mass conservation. From the 400 fruit flies that we released in the simulations, after a few time steps only a dozen or so were left.

Therefore, we decided to renounce modelling chemotaxis at the population level (as we did for the other chapters of this thesis) and tried an individual-based approach for fruit fly movement instead. The filamentous plume model describes the movement of individual odour filaments stochastically in an environment with spatial and temporal variation in local wind directions and speed (Farrell et al., 2002). Thus, using a stochastic model for fruit fly movement that is also individually based proved to be the solution for all the numerical problems that we faced. In hindsight, it is logical that the IDE method for fruit fly dispersal can only be used in combination with the Gaussian plume model or normal distribution of odours, as they both use time-averaged distribution patterns. Moreover, it is also logical that the stochastic filamentous plume model needs a stochastic approach for fruit fly movement.

6.4.2 Modelling odour discrimination

To our knowledge, modelling of odour plume tracking has focussed only on behavioural rules that animals or autonomous agents use to track one odour plume (Sabelis and Schippers, 1984; Weisburg et al., 2002; Yamanaka et al., 2003; Kowaldo and Russell, 2008). In reality, animals often are in a situation where several odour sources are present that differ in attractiveness. In this chapter, we investigated which behavioural decisions enhance the ability to find - and distinguish between – different odour sources. Starting point for our individual-based model for fruit fly movement was an individual-based model for sex-pheromone oriented flight of male moths (Yamanaka et al., 2003), that we parameterized for *D. melanogaster* (Budick and Dickinson, 2006). Fruit flies in this basic model were not able to discriminate between odour sources containing only food odours or both food odours and aggregation pheromone. In the incentive model, fruit flies had a preference for tracking a plume with odour concentrations similar or higher than they had sensed recently. This behaviour enhanced the probability that a fruit fly arrived at an "F+A" source, however there was a large variability in the number of fruit flies that arrived at the "F+A" source. Fruit flies in the motivation model also had a preference tracking a plume with odour concentrations similar or higher than they had sensed recently, but in this model they had an innate preference for the presence of aggregation pheromone. In the motivation model, the threshold value was set in such a way that fruit flies only perceive the odours when aggregation pheromone is present. This resulted in lower arrival at the odour sources, but also in smaller variability of the results. Therefore, using a threshold value that is higher than in the incentive model, but lower than in the motivation model could potentially better simulate the higher arrival found at "F+A" and the low variability in the field experiments. In the downwind model, with behavioural rules based on the incentive model, fruit flies now fly downwind when they lose contact with the plume and do not find the plume back within three zigzag movements (Kellog et al., 1962). This behaviour greatly enhanced their ability to discriminate between odours and to arrive at the odour source that contained both food odours and aggregation pheromone, resulting in a much higher arrival at the "F+A" sources than actually found in the field experiment of Wertheim et al. (2002a). If in the downwind model the preference for "F+A" over "F" (η in Eq. 11) would be weaker it could also potentially model fruit fly arrival better. Future research should address a parameter estimation for the "incentive model" and the "downwind model" to find the parameter combination that best describes the distribution of arrived fruit flies found in the field experiment of Wertheim et al (2002a). That the incentive model gives better results than the motivation model shows that the strength of the preference for "F+A" over "F" does not have to be innate, as long as fruit flies are able to remember (Yin et al., 2010) and adjust their current preference of "F+A" over "F" (Bruce et al., 2005). This is also what one would expect, as odour sources that only contain food odours are potentially suitable for reproduction. In an environment where no aggregation pheromones are present yet, all fruit flies are attracted to only food odours and have opportunities to meet other individuals there. Only from the moment that the odour sources start emitting aggregation pheromone – an indication that other fruit flies are or have been there – these "F+A" sources become the more suitable odour sources.

Spatial distribution

We modelled odour distribution in a 2D plane, with transport only in a horizontal plane. But in reality, odour filaments do not only disperse in a 2D-plane, they also disperse in the vertical direction (Elkington and Cardé, 1984). When an odour filament leaves the source, its vertical position may increase gradually. This causes an additional decrease of the odour concentration in a plume, as the distance to its source increases. This effect is not properly incorporated into our 2D model, where the odour plumes from more distant upwind sources overlap the odour plumes from more nearby upwind sources to a greater extent than they do in reality. Moreover, the ability of fruit flies to trace the vertical centre line of an odour plume towards the source (Budick and Dickinson, 2006) cannot be implemented in a 2D model. Therefore, in reality when a fruit fly moves more upwind than the odour source of the plume it was tracking, an individual would lose contact with the odour plume and start zigzag flight. In our simulations, fruit flies continue flying upwind because there still is odour present from the odour sources upwind. This can be the reason why in our model most fruit flies arrive at the most upwind odour sources which are positioned furthest away from the fruit fly release point, while, in the cage experiment they predominantly arrived at the odour sources closest to the release point. Including the vertical dimension in the models could improve the spatial distribution of fruit fly settlement, but would also increase both the complexity of the models and the runtime. One repetition of the “R8” simulation, modelling 400 fruit flies for 30 minutes, took 30 hours to run. The “R2” simulations, modelling 400 fruit flies for 10 minutes, were faster, but still took 4.5 hours to simulate. The main factor slowing the simulations down was the modelling of the odour plumes with the filament plume model.

Vision

Many insects rely on visual feedback to fly upwind (Kennedy, 1940; Kellog et al., 1962; Kennedy and Marsh, 1974; Frye et al., 2003). Furthermore, fruit flies use visual stimuli to localize odour sources (Frye et al., 2003; Tammero and Dickinson, 2002; Stewart et al., 2010). Even though we developed a “vision” model, it is a very crude model that only affects the zigzag speed in the proximity of the odour source, and not the direction of the flight. If we would like to model vision properly, we need a 3D model for odours and the visual environment and a complicated model for visuomotor control, including stabilizing yaw orientation, collision avoidance and speed regulation (Stewart et al., 2010). There is a trade-off between modelling odour plumes and visual arenas explicitly. In our model, we modelled odour distribution in a large domain and fruit fly responses to odours explicitly, and simplified the visual feed-back. Stewart et al. (2010) modelled the visual arena and fruit fly responses to visual input explicitly in a small domain and used a simplification for odour distribution.

6.4.3 Conclusion

The models that we developed show what behavioural responses are important for discriminating between odours and tracking an odour plume towards its source. When fruit flies had a preference for tracking a plume with odour concentrations similar to or higher than those sensed recently, this enhanced the number of fruit flies that arrived at the preferred odour source that emits both food odours and aggregation pheromone. Furthermore, the arrival at the “F+A” source even more increased when fruit flies were able to move downwind when during zigzag flight contact with the plume was not recovered soon after loss with the odour plume. Furthermore, our models show potential for estimating how many fruit flies arrive at the “F+A” and “F” sources. However, they were not able to predict the spatial distribution of the fruit flies over the different odour sources correctly. Including the vertical dimension in the models could improve the spatial distribution of fruit fly arrival. This remains a challenge for future research.

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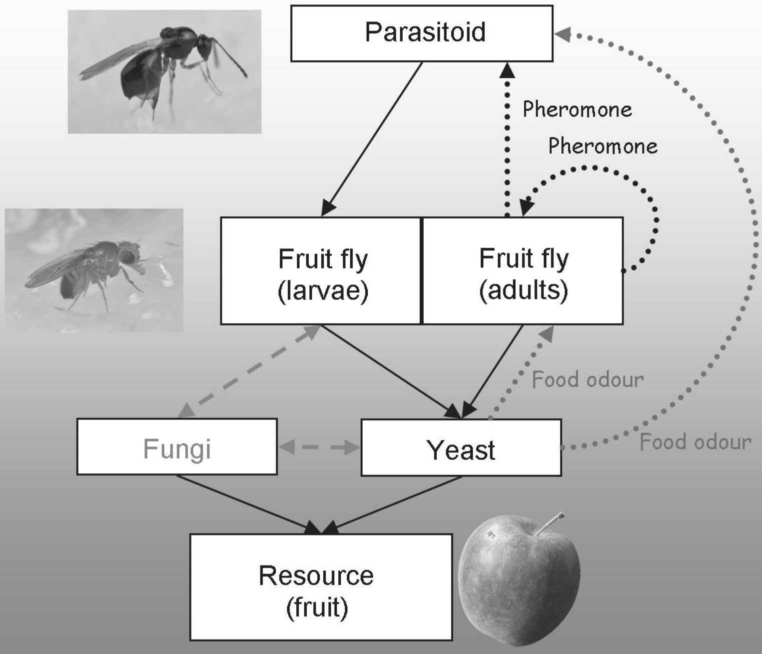
Chapter 7



Pictures Hans Smid (Bugsinthepicture.com)

General discussion

Marjolein E. Lof

7.1 Introduction

Many species ranging from microbes to mammals use odours to communicate (Bell and Cardé, 1984; Wyatt, 2004; Kats and Dill; 1998, Dicke and Takken, 2006). For instance; many territorial mammals (like tigers and wolves) use urine to mark the boundaries of their territory, female moths emit sex pheromones that can attract male moths over large distances (Wall and Perry, 1987; Ostränd and Anderbrant, 2003). Such communication is often restricted to communication between individuals of the same species. However, other species may respond to the odours that are emitted as well. For instance, parasitoids are attracted to sex pheromones or aggregation pheromones emitted by their hosts (Vet & Dicke, 1992; Hedlund et al., 1996; Dicke et al., 1994; Fatouros et al., 2008). Thus a wide range of volatile substances transfer information, hence they are called infochemicals (Dicke and Sabelis, 1988). Once an infochemical is emitted, in principle any organism can exploit its information. Infochemicals can thus provide information on the presence of competitors or natural enemies, as well as the availability of food or mates. Infochemicals affect the dispersal and distribution of organisms, the distribution of competing species and natural enemies, and, consequently, they may have an impact on the population dynamics of species in the food web. Yet, the study of chemical information use has been mostly restricted to the level of individual organisms and the identification of chemical substances that convey the information. The central question in this thesis is: How does the use of chemical information influence the population dynamics of and the interactions between species at consecutive trophic levels in a food chain? At a more detailed level is also investigated why a host species uses an aggregation pheromone when aggregating can result in increased competition among conspecifics for a limited food source, or when the communication used to aggregate can be spied upon by a natural enemy. The fruit fly *Drosophila melanogaster* and its natural enemy, the larval parasitoid *Leptopilina heterotoma* are used as model system. *D. melanogaster* uses an aggregation pheromone in combination with food odours to find a resource that is suitable for oviposition. *L. heterotoma* uses these same infochemicals to find its host, the larvae of the fruit fly. The models in this thesis are specifically focused on studying the effect of the use of chemical information on the population dynamics of the host. To answer the above questions, a modelling approach was used. By using simulation models, the effect of changing variables that are difficult to estimate by direct experiments can be investigated, while at the same time other factors can be kept constant.

7.2 Model techniques and assumptions

A model is a simplification of reality. Every model and modelling technique has its own advantages and disadvantages. Therefore, an important aspect of modelling is to choose a model that comprises the features that are essential for solving the specific questions to be addressed. What is important depends on the aim of the model and the temporal and spatial scale of interest. In this thesis, the population dynamics of the fruit fly (i.e. population growth) is addressed, which occurs on a time scale of several generations (i.e. one year), but also the process of fruit fly searching for and settling on a suitable resource, which is at a scale of milliseconds to minutes. Thus, there are large differences in the temporal scale of the relevant processes. The same is true for the spatial scale; the fruit fly movement is in the range of tens of meters, while the small bursts of odour that are emitted by the odour source represent a process at a scale in the range of millimetres. **Chapters 2-5** mainly address the population dynamics of the fruit fly. With this goal in mind, the proper approach is not to explicitly model the small scale processes of odour distribution and individual movement, but to model the odour distribution and fruit fly dispersion as an average distribution over a longer time period. In **Chapter 6**, the behavioural decisions of the fruit flies while searching for, and distinguishing between, different odour sources are addressed. Therefore, this was modelled on a smaller time scale of milliseconds and only addressed the odour distribution and fruit fly arrival on the odour-emitting patches for 30 minutes.

For **Chapters 2-5**, an integro-difference approach (as in Neubert et al., 1995; Powell et al., 1998) was used. In this approach, fruit fly dispersal and reproduction (e.g., reproduction) are treated as two distinct phases; the odour and fruit fly dispersal are modelled separately from the adult population dynamics. This allows the numerical simulation to take larger time steps without running into numerical stability problems. Based on Powell et al. (1998), I assumed that the relevant processes of infochemical and fruit fly dispersal could be modelled efficaciously in a 2D plane. To account for the fact that odours also diffuse in the vertical plane, we introduced a loss rate for the fraction of odour that gets out of reach of the searching fruit flies (e.g. diffuses above two meters high). For a spatio-temporal model of *Drosophila,* based on responses to food odours and aggregation pheromone, realistic parameter values were (and still are) hard to obtain. Therefore, the parameterization of the model in **Chapter 2** (where we modelled fruit fly population dynamics when they could use chemical information in the absence of a natural enemy) is discussed in **Chapter 3** and combined with a sensitivity analysis.

For a long time, the spatial aspects of parasitoid-host systems have received little or no attention. However, work by Tilman and Kareiva (1997), and Turchin (1998) showed that spatial aspects can be very important. Modelling studies that include spatial effects mainly focused on optimizing searching strategies (foraging behaviour) in environments where resources are heterogeneously distributed (Charnov, 1976; Haccou et al., 1991; Bukovinszky et al., 2007). Other modelling studies on population dynamics in parasitoid-host systems focused on temporal stability or on spatio-temporal patterns (Ives, 1992; Hirzel et al., 2007; Nguyen-Huu, et al., 2006; Pearce et al., 2007; Schofield et al., 2005). There are few studies that model the effect of chemical information on spatio-temporal parasitoid-host dynamics. Puente et al. (2008), Pearce et al. (2007) and Schofield et al. (2002) studied the effects of chemical information; however, in these studies only the parasitoid response to chemical information, i.e. herbivore-induced plant volatiles, was addressed, whereas the response of the herbivorous host to chemical information was not included. A novel aspect of **Chapter 5** is that both the host and its natural enemy can respond to chemical information. Driven by the aim to investigate the costs and benefits of aggregation pheromone use by fruit flies when an enemy is spying on their communication, the focal species in **Chapter 5** is the host, the fruit fly. As a consequence, parasitoid reproduction and long term population dynamics were not modelled explicitly. As for **Chapters 2-4**, we used integro-difference modelling, but, as is convention for parasitoid-host models, the equations were written as difference equations.

As mentioned above, every model and modelling technique has its own advantages and disadvantages. The research presented in **Chapter 6** started by modelling fruit fly movement in realistic time-varying odour plumes with the integro-difference model (IDE) for fruit fly distribution used in **Chapters 2-5**. Although the IDE method for fruit fly dispersal works nicely in combination with the time-averaged distribution patterns for odour dispersal used in **Chapters 2-5**, it did not work for an instantaneous odour plume model, with large variation in odour concentrations both in the temporal and the spatial scale (even with very small spatial and temporal steps). The advantage of using the IDE approach over other numerical approaches is that it can use large time steps to approximate the spatial distribution and therefore can calculate population distributions faster than other numerical approaches (Powell et al., 1998). By using a very small time step, the IDE approach loses the advantage of faster calculations and its error increases, because a higher number of approximations are needed to calculate the population distribution.

Therefore, it was decided to renounce modelling chemotaxis at the population level and to adopt an individual-based approach for fruit fly movement instead. The realistic plume model describes the movement of individual odour filaments stochastically in an environment with spatial and temporal variation in local wind directions and speed (Farrell et al., 2002). Thus, using a stochastic model for fruit fly movement that is also individually based proved to be the solution for all the numerical problems that we faced. In hindsight, it is very logical that the IDE method for fruit fly dispersal can only be used in combination with a realistic distribution of odours, as they both use time-averaged distribution patterns. Moreover, it is also logical that the stochastic filamentous plume model needs a stochastic approach for fruit fly movement.

In this thesis, odour distribution was modelled in a 2D plane, with transport only in a horizontal plane. But in reality, odour filaments do not only disperse in a 2D plane; they also disperse in the vertical direction (Elkington and Cardé, 1984). When an odour filament leaves the source, its vertical position may increase gradually. This causes an additional decrease of the odour concentration in a plume, as the distance to its source increases. This effect is not properly incorporated in our 2D model. In **Chapters 2-5** the odour plume originating from one resource overlaps with the odour plumes originating from nearby resources. This results in a more evenly distributed settlement of the fruit flies over the available resources, as they will also settle on a resource that was not emitting aggregation pheromone itself but was in close proximity of another resource that was emitting aggregation pheromone. Because the odour distribution was modelled in only two horizontal dimensions, odour plumes that would be vertically separated in the 3D reality may overlap in the model. Therefore, the fruit flies in the model are not able to discriminate between an aggregation-pheromone-emitting resource and a resource that lies within the aggregation pheromone distribution originating from another resource. When the population is small, this can cause an underestimation of the positive effect of aggregation, by a decreased Allee effect. On the other hand, when the population is large it can overestimate the negative effect of competition.

Also in **Chapter 6**, the odour plumes from more distant upwind sources overlap with odour plumes from more nearby upwind sources to a greater extent than they do in reality. Moreover, the ability of fruit flies to trace the vertical centre line of an odour plume towards the source (Budick and Dickinson, 2006) cannot be implemented in a 2D model. Therefore, in reality when a fruit fly moves more upwind than the odour source of the plume it was tracking, an individual would lose contact with the odour plume and start zigzag flight. In our simulations, fruit flies continue flying upwind because there still is odour present from the odour sources upwind. This can be the reason why, in our model, most fruit flies arrive at the most upwind odour sources (**Chapter 6**), which are positioned furthest away from the fruit fly release point, while, in the cage experiment they predominantly arrived at the odour sources closest to the release point (Wertheim et al., 2002a). Including the vertical dimension in the models could improve the spatial distribution of fruit fly settlement, but would also increase both the complexity of the models and the runtime. One simulation run with eight odour sources, modelling 400 fruit flies for 30 minutes, took 30 hours of computer time. While one simulation with two odour sources, modelling 400 fruit flies for 10 minutes, were faster, but still took 4.5

hours to simulate. The main factor slowing the simulations down was the modelling of the odour plumes with the filament plume model.

Many insects rely on visual feedback to fly upwind (Kennedy, 1940; Kellog et al., 1962; Kennedy and Marsh, 1974; Frye et al., 2003). Furthermore, fruit flies use visual stimuli to localize odour sources (Frye et al., 2003; Tammero and Dickinson, 2002; Stewart et al., 2010). The “vision" model developed in **Chapter 6** is a very crude model that only affects the zigzag speed in the proximity of the odour source, and not the direction of the flight. To model vision properly, one needs a 3D model for odours and the visual environment and a complex model for visuomotor control (Stewart et al., 2010). Due to the complexity of both the olfactory and visual cues and the subsequent behaviour, there is a trade-off between modelling odour plumes and visual arenas and the individual responses thereupon explicitly. In **Chapter 6**, odour distribution was modelled in a large domain and fruit fly responses to infochemicals were modelled explicitly, and the visual feed-back was simplified, while Stewart et al. (2010) modelled the visual arena and fruit fly responses to visual input explicitly in a small domain and used a simplification for odour distribution.

7.3 Chemical communication – The use of chemical information affects fruit fly population dynamics

Chapters 2 and **4** report that the use of chemical information affected fruit fly population dynamics in the simulations. In **Chapter 2** the initial fruit fly population was situated in the centre of the orchard. Before they can reproduce they must re-colonize their natural habitat in spring. In reality, fruit flies hibernate outside the breeding area (Boulétreau-Merle et al., 2003). At the end of the winter, only a fraction of the original population has survived. Before they can reproduce, they must re-colonize their natural habitat in spring. Therefore, in **Chapter 4** the effect of chemical information was investigated when the fruit flies had to colonize the orchard from its boundaries. In both situations, the use of infochemicals had a positive effect on population growth when the fruit fly population was small. When fruit flies could use chemical information, the settlement of adult fruit flies was higher than when they could not use chemical information. This higher settlement, which is in the model directly associated with more eggs being laid, reduced the local larval mortality due to the Allee effect. When the population was small, the positive effects of reduced mortality due to the Allee effect outweighed the negative effects of increased mortality due to competition. The number of offspring that survived was higher in the presence of infochemicals. When fruit flies had to re-colonize the area from outside, the use of chemical information was crucial for the colonization of the area. A randomly dispersing population – that could not use chemical information – was not able to colonize the area that contained the apples. During colonization of an area, populations that cannot use chemical information suffer from extremely high larval mortality (>90%) due to the Allee effect. This was mainly because these populations had more difficulties in locating a resource and were not able to aggregate on suitable resources. When there was an Allee effect on larval survival, the randomly dispersing population went extinct. In **Chapter 4**, the population dynamics were also simulated without an Allee effect, i.e. high mortality at low larval densities, present. The data show that even without an Allee effect, the randomly dispersing population could not colonize the orchard successfully. This showed that for fruit flies it is essential to use chemical information – especially that from the aggregation pheromone – when colonizing an area.

The results presented in this thesis indicate that the use of chemical information is especially useful when the population is small, mainly because aggregation by the adult fruit flies reduced the local mortality due to the Allee effect in their larvae (**Chapters 2** and **4**). In *D. melanogaster* adult aggregation has a positive effect on larval survival because adults alter the suitability of the resource for the juveniles. Adults, especially females, vector a diversity of yeasts and inoculate the resource with these yeasts during their presence (Morais et al., 1995). As fruit fly larvae feed on yeast, inoculation of the resource with yeast increases the amount of food for the larvae. At the same time, this increase in yeast also reduces fungal growth (Wertheim et al., 2002b). This positively affects larval survival, because strong fungal growth can cause a high mortality in fruit fly larvae (Rohlfs et al., 2005; Rohlfs, 2006). Furthermore, larger groups of larvae are more successful at suppressing fungal growth by disrupting the hyphae of the fungus than smaller groups or single larvae (Rohlfs et al., 2005; Rohlfs, 2008). The local interaction of larvae and yeast with the fungi thus gives rise to an Allee effect in larval development.

Infochemicals guide fruit flies towards the resources and, thereby, can have a positive effect on population numbers by decreasing the mortality due to the Allee effect. On the other hand, when too many fruit flies are attracted, the carrying capacity of an apple can be exceeded which will result in a higher larval mortality due to competition for food. The mortality due to competition can be quite severe especially when the attraction towards chemical information is high: 40-60% larval mortality. High mortality due to competition does, however, not have the same dramatic effect on population size as mortality due to the Allee effect. The data in **Chapter 2** show that for mortality due to competition varying between 50-55%, the population size remained approximately constant. When mortality due to competition was higher than 55%, the population decreased and when it was lower than 50% the population increased. Nonetheless, at the individual level the costs of using chemical information can be severe.

Hoffmeister and Rohlfs (2001) experimentally showed that fruit flies often misjudge the carrying capacity of resources and not only aggregate their eggs when confined to a limited amount of resource items (when it would be appropriate) but also when resources are not a limiting factor. A possible explanation could be that food patches are not always abundant. As was found in **Chapters 2** and **4**, mortality due to the Allee effect had a larger impact on population size than mortality due to competition. As a result, having difficulties in finding a resource has a more negative effect on population persistence than clumping too much. Therefore, the reproductive success of fruit flies is mainly determined by their opportunities of producing clutches (i.e. locating patches) rather than optimal egg-laying decisions.

It seems contradictory that fruit flies use chemical information when there are clearly costs involved. Yet, if we take into account that our simulated fruit fly population that was subject to an Allee effect and could not use chemical information was unable to colonize the orchard and became extinct within 4 generations, the ability to use chemical information is beneficial when an area has to be re-colonized at the start of each new breeding season. In reality, the resources that fruit flies use are ephemeral; this means that they are only present for a short time. Furthermore, many fruit species are only overripe for a short period in the season. Therefore, the life of a newly emerged adult generally starts with localizing a new resource suitable for reproduction. Under these conditions, the ability to find and colonize a new area is even more important.

7.4 Chemical espionage – Spying enemies affect fruit fly population dynamics

Predators and parasitoids commonly use chemical cues associated with herbivore feeding (upon infestation many plant species are known to produce volatiles that attract predators and parasitoids) and cues that are associated with reproduction (for instance sex pheromones of their prey) to locate prey (Turlings et al., 1995; De Moraes et al., 1998; Shiojiri et al., 2001; De Boer and Dicke, 2004; Fatouros et al., 2005; Bruinsma and Dicke, 2008; Hare, 2011). The exploitation of chemical cues of the host or the host's habitat by predators or parasitoids often results in a higher attack or parasitism rate (Wertheim et al., 2003; but see Tentelier and Fauvergue, 2007). In **Chapter 5,** the effect of chemical information on the interaction between hosts and parasitoids is examined for a system where *L. heterotoma* spies on the intra-specific communication of *D. melanogaster*. I studied whether the use of chemical information is still beneficial for the fruit flies when a natural enemy is present that can spy on its intraspecific communication.

Effects of the use of chemical information by the host

Consistent with **Chapters 2** and **4**, it was found that the use of chemical information by the fruit flies enhanced their own population growth rate, even when parasitoids are present. In addition, **Chapter 5** reports that fruit flies that use chemical information, i.e. food odours and the aggregation pheromone, could persist with more parasitoids present than in the situation where they only dispersed randomly. When fruit flies used chemical information, more fruit flies found the resources. Therefore, more eggs were laid per resource, resulting in a lower percentage mortality due to the Allee effect. Through this reduction in percentage mortality due to the Allee effect, the population was able to survive higher parasitism pressure.

Effects of spying parasitoids

Chapter 5 shows that the exploitation of chemical information by the parasitoid negatively affected the size and growth of the fruit fly population. In accordance with experimental results of Wertheim et al. (2003) for the same experimental system, the modelling study found that when parasitoids exploited chemical information the average parasitism rate was higher. As a result, the population growth rate of the fruit flies was lower. Therefore, it took longer to overcome the negative effects associated with a small population size – the Allee effect. Moreover, this negative effect was stronger when fruit flies were not able to use chemical information and had to find the resources by random dispersal.

A mechanism by which aggregation can be advantageous is that at high population densities individuals can experience a diluted risk of attacks by their natural enemies (Parrish and Edelstein-Keshet, 1999; Wertheim et al. 2005). Rohlfs and Hoffmeister (2004) indeed show that risk of parasitism can decrease with increasing larval density. However, this was mainly because at higher larval densities the larvae could move deeper into the resource, which provides a spatial refuge against larval parasitoids. This was not possible in our simulation set-up. The simulations did not provide evidence for a locally diluted risk of parasitism at higher larval densities. In contrast, the simulations showed that larval mortality due to parasitism increased with larval density on a resource. A likely explanation is that the patch residence time of *L. heterotoma* is positively related to the number of hosts present on the patch (Van Lenteren and Bakker, 1978). When the fruit fly population is large, the larval densities on the resources are high, and *L. heterotoma* spends a long time foraging at that resource item.

Ecological costs of chemical communication

Predation and parasitism are important mortality factors for many insect herbivores. Predators and parasitoids often use chemical information to locate their prey or hosts. This is especially advantageous for natural enemies that search for cryptic prey. Predation and parasitism are expected to exert a strong selective pressure on intra-specific communication by chemical information. Nevertheless, because pheromones are crucial to many aspects of herbivore life history, alterations of these compounds could be disadvantageous despite their exploitation by predators and parasitoids (but see Raffa et al., 2007).

In *Drosophila*, larval parasitism is an important mortality factor (Janssen et al., 1988; Allemand et al., 1999; Wertheim et al., 2003; Fleury et al., 2004). The larval parasitoid *L. heterotoma* exploits the aggregation pheromone of the adult fruit flies to localize its hosts. I, therefore, expected that the use of aggregation pheromone by *D. melanogaster* would increase the percentage mortality due to parasitism in the larvae of *D. melanogaster*, as was also found in the field (Wertheim et al., 2003). To test the hypothesis that fruit flies experience an additional cost associated with the use of aggregation pheromone as a result of an increased mortality due to parasitism, fruit fly population dynamics in the case that the parasitoid can only use odours emitted by the host habitat, i.e. food odours, were compared to the case where the parasitoid can use both odours emitted by the host habitat and the aggregation pheromone of the fruit flies. The results indicate that for *D. melanogaster* there is no additional cost, with respect to an increased risk of parasitism, for the use of aggregation pheromones. No difference was recorded in fruit fly population size and in larval mortality due to parasitism, when parasitoids exploited the aggregation pheromone of the fruit fly adults as compared with the simulations where the parasitoids could only respond to chemicals emitted by the host habitat. In contrast, the use of chemical information by the host enhanced its population growth and enabled it to survive, even at higher parasitoid densities. As a result, the use of chemical information has a net positive effect on fruit fly population dynamics, despite the fact that *L. heterotoma* is able to exploit it.

However, this does not imply that there is no cost with respect to parasitism when parasitoids can respond to chemical information. The fruit fly population increased at a slower rate (both for the fixed number and the fixed fraction of parasitoids) and had a lower carrying capacity (only at a fixed fraction of parasitoids) when parasitoids could use chemical information as compared to the simulations where they could only search randomly. This, however, is already the case when parasitoids could only respond to food odours. In this respect, the risk of parasitism by *L. heterotoma* responding to food odours is comparable to the risk of parasitism in a system where parasitoids exploit herbivore-induced plant volatiles (DeMoraes et al., 1998) or odours from microbial symbionts (Boone et al., 2008) to locate their hosts. It is important to note that the presence of food odours is not something that the fruit flies are likely to 'control'. The most attractive compounds in the food odour blend for fruit flies are the volatiles that are produced by fermentation by the yeasts (Hutner et al., 1937), and yeasts are an important food source for the larvae of the fruit fly.

The models in this thesis were parameterised for *D. melanogaster* and in **Chapter 5** for the interaction between *D. melanogaster* and *L. heterotoma*. With some adjustments these models are also applicable to other systems, as many species use aggregation pheromones (reviewed in Wertheim et al., 2005) or sex pheromones to communicate with conspecifics and also the exploitation of these infochemicals by a natural enemy is quite common (Vet & Dicke, 1992; Hedlund et al., 1996; Dicke et al., 1994; Fatouros et al., 2005a; Fatouros et al., 2008). I expect that the use of aggregation pheromones in the absence of competitor species or natural enemies in general will have a positive effect on population dynamics, as our results indicate in **Chapter 2 and 4**. The effect of exploitation of infochemicals by a natural enemy is dependent on the patch-leaving mechanism. In parasitoids, an encounter, oviposition or host rejection can have a positive, a negative or no effect on the patch leaving tendency (Wajnberg, 2006; Varaldi et al., 2005; Kolss et al., 2006). Furthermore, some species have an innate response to infochemicals, while others learn to respond to infochemicals after a successful oviposition (Hedlund et al., 1996). These different responses to odours and to encounters can affect the density dependency of the parasitism rates by the natural enemy. Van Lenteren and Bakker (1978) and Varaldi et al. (2005) showed that patch residence time of *L. heterotoma* increases with increasing larval density. Furthermore, from the presence of host kairomones *L. heterotoma* can assess the larval density at the patch when it arrives (Dicke et al., 1985). For high larval densities, this results in long duration on the patches and in high parasitism rates. Parasitoids for which a successful oviposition has a negative effect stay shorter at a resource and thus could have a different relation between parasitism rate and larval density (and possible a diluted risk of attack).

7.5 Chemical discrimination – Finding the most suitable source

Chemical information becomes available to flying insects when molecules are distributed into the environment by wind and turbulent diffusion. In **Chapter 6** five individual-based models for odour-oriented flight patterns of individual fruit flies were introduced. In these models, fruit flies were allowed to respond to a filamentous plume model (Farrell et al, 2002), that takes many features of a real odour plume into account. To my knowledge, modelling of odour-plume tracking has focused only on behavioural rules that animals use to track one odour plume (Sabelis and Schippers, 1984; Weisburg et al., 2002; Lo Iacono, 2010). In reality, animals often are in a situation where several odour sources are present that differ in attractiveness. In **Chapter 6**, I investigated which behavioural decisions enhance the ability to find - and distinguish between – different odour sources. Starting point for the individual-based model for fruit fly movement was an individual-based model for sex-pheromone oriented flight of male moths (Yamanaka et al., 2003), that we parameterized for *D. melanogaster* (Budick and Dickinson, 2006). Behavioural decisions of moths could be used for odour tracking of fruit flies in a filamentous odour plume. Fruit flies need to have a preference for the combination of food odours and aggregation pheromone, over food odours in absence of aggregation pheromone, to be able to distinguish the most suitable odour source (e.g. “F+A”). However, this stronger preference does not have to be set in advance. As long as fruit flies are able to remember (Yin et al., 2010) and adjust their current preference of “F+A” over “F” (Bruce et al., 2005) based on the odour concentrations of food odours and aggregation pheromone that they perceive, more fruit flies find the more attractive odour source. This is also what one would expect, as odour sources that only contain food odours are potentially suitable for reproduction. In an environment where no aggregation pheromones are present yet, all fruit flies are attracted to only food odours and have opportunities to meet other individuals there. Only from the moment that the odour sources start emitting aggregation pheromone – an indication that other fruit flies are or have been ovipositing there – these “F+A” sources become the more suitable odour sources. Furthermore, when fruit flies fly downwind when they lose contact with the plume and do not find the plume back within three zigzag movements (Kellog et al., 1962), this behaviour greatly enhanced their ability to discriminate between odours and to arrive at the odour source that contained both food odours and aggregation pheromone, resulting in a much higher arrival at the "F+A" sources.

The outcome of the models was compared to experimental data of Wertheim et al. (2002a). The models show potential for estimating how many fruit flies arrive on the "F+A" and "F" sources. However, in the field experiment by Wertheim et al. (2002a) the fraction of fruit flies that arrived at an odour source decreased with distance from the release point, while in the simulations the opposite was found. In the simulations, the odour sources that were furthest away from the release point attracted the most fruit flies. Although the models were successful in estimating how many fruit flies settle on the "F+A" and "F" sources, they were not able to predict the spatial distribution of the arrivals correctly. This remains a challenge for future research.

7.6 Future directions

In general, any population model for the response of insects to volatile infochemicals in the air can be divided into three parts:

1. A model for insect behaviour where the population members are divided among states depending on their activity.
2. A model for production, evaporation and dispersion of the odour substances.
3. A model for the detection of odours by insects, and their reaction thereupon.

The parameterization of these sub-models requires input from quite different disciplines.

The first sub-model lies in the field of behavioural ecology. Based on thorough study on the *Drosophila*-based food web (e.g. Wertheim, 2001) the population members were categorized into three activity states. However, quantitative measures of the rate at which the searching flies in the close vicinity of a resource item settle, the rate at which the settled flies leave the resource, and the rate at which moving flies start searching again still lack. The same applies to oviposition rates of *Drosophila*. As these parameters model population processes that have their roots in individual insect behaviour, more accurate estimates should be made available from insect behavioural experiments, either in artificial setups, or in the field, or both.

The second sub-model lies in the field of physics, organic chemistry and micro-meteorology. Although many models exist for odour transport, most models are developed for large scale and time-averaged odour distribution. Models for plume transport on short and intermediate distances need further investigation. Our results (**Chapters 2-6**) indicate that modelling odour dispersion and fruit fly responses thereupon in 2D has an effect on the ability for the fruit fly to distinguish the source from the odour it is tracking from another source that it encounters on its way to the other source. Further research should be conducted to investigate to what extent the results from a full 3D spatial model for insect behaviour agree with the results that we recorded with the present, essentially 2D, model.

The third sub-model lies in the field of biophysics and neurology. This sub-model may be the most challenging. Although some knowledge exists on how fruit flies react to aggregation pheromone (Wertheim et al., 2002), nothing is known about the spatial dose-response relationship to food odours and aggregation pheromone. In the model for the reaction of fruit flies to infochemicals that we used, two parts may be distinguished: the sensory index function that describes the perception of our virtual fruit flies to infochemicals, and an additional parameter ν, describing the strength of chemotaxis as compared to random walk movement. At this moment, quantitative data are so scarce that this submodel is clearly overparameterized. We have solved this problem by fixing a combination of the parameters ν and η, the ratio of the strength of the attraction to food odours in combination with aggregation pheromone over the attraction to food odours in absence of aggregation pheromone. It will not be easy to decouple these parameters just by ethological experiments, as this would require a very controlled setup to establish a quantitative relation between fruit fly behaviour and measured infochemical concentration gradients.

We used a Michaelis-Menten type of function for saturated response of the fruit fly to the two infochemicals (e.g. food odours and aggregation pheromone). For a sensory index function for one infochemical, the use of a Michaelis-Menten type of function for saturated response can be made plausible from the limited availability of sensory nerve cells to accommodate infochemical molecules (e.g. Postma, 2003). However, for two interrelated infochemicals, many types of sensory index functions are conceivable, and we have chosen a simple one from them. It may require neurological research on fruit flies to validate this choice.

The parameter estimation and sensitivity analysis in **Chapter 3** indicated that insight into the spatial ecology of aggregation should be derived from a multidisciplinary approach that includes the identification of the cues that mediate aggregation, the behavioural responses of individuals to these cues, and the spatial variation in the responses that result from spatial variation in pheromone distribution. With the results of the sensitivity analysis in mind, especially reliable estimates for the parameters that describe the diffusion of the infochemicals, the dispersal of the fruit flies and the patch leaving rate of the fruit flies of are required. Furthermore, the results from **Chapter 5** the patch leaving rates the parasitoids seem to be important too. Testing the effect of varies patch leaving rules can give more insight in the costs of parasitism for different types of parasitoids.

Within the set of individual-based models developed in **Chapter 6**, the incentive and the vision model showed the smallest deviation from the real data. In the incentive model, fruit flies had a preference for tracking a plume with odour concentrations similar or higher than they had sensed recently. This behaviour enhanced the probability that a fruit fly arrived at an "F+A" source. However, there was a much larger variability in the number of fruit flies that arrived at the "F+A" source than was found in the field experiment by Wertheim et al. (2002a). In the motivation model, the threshold value was set in such a way that fruit flies only perceive the odours when aggregation pheromone is present. This resulted in lower arrival at the odour sources, but also in smaller variability of the results. Therefore, I put forward using a threshold value that is higher than in the incentive model, but lower than in the motivation model could potentially better simulate the higher arrival found at "F+A" and the low variability in the field experiments.

Resource location by both olfactory and visual cues in fruit flies is an exciting new research area. In the last decade many papers have been published on experimental studies that address both cues (Frye et al., 2003; Tammero and Dickinson, 2002; Stewart et al., 2010; Chow et al., 2011). Awareness is growing that neither visual cues nor olfactory cues alone are sufficient to recognize and locate a suitable resource (Chow and Frye, 2009). A major challenge lies in using the most important features of olfactory and visual cues that the fruit flies use and combining these new insights into a single model that can describe resource location in a complex world.

The present study provides the first step in unravelling the effect of infochemical use on population dynamics of *D. melanogaster* when the infochemicals can be exploited by one of its natural enemies, the larval parasitoid *L. heterotoma*. In reality, the food web of *D. melanogaster* is more complex. There are closely related drosophilid species that use the same aggregation pheromone (Schaner et al., 1987; Hedlund et al., 1996; Symonds and Wertheim, 2005) and there are other natural enemies that could potentially exploit these infochemicals (Hedlund et al., 1996). Furthermore, the Allee effect seems to arise from the interaction with yeasts and fungi (Wertheim et al., 2002b; Rohlfs et al., 2005, Rohlfs, 2008). Research on the effect of competition between closely related fruit fly species and local competition between the larvae and the fungi and the yeast could further complement the picture of the ecological costs and benefits of infochemical use in a small food web.

References

Allee, W.C., 1931. Animal aggregations, a study in general sociology. University of Chicago Press, Chicago.

Allemand, R., Fleury, F., Lemaître, C., Boulétreau, M., 1999. Population dynamics and competitive interactions in two species of Leptopilina (Hymenoptera : Figitidae) which parasitize *Drosophila* in the Rhone valley (S-E France). Annales de la Société Entomologique de France 35, 97-103.

Allen, J.C., Brewster, C.C., Slone, D.H., 2001. Spatially explicit ecological models: a spatial convolution approach. *Chaos Soliton. Fract.*12 (2), 333-347.

Ashburner, M., Golic, K.G., Hawley, R.S., 2005. *Drosophila*: A Laboratory Handbook. (2nd ed.). Cold Spring Harbor Laboratory Press, pp. 162–164.

Atkinson, W.D., Shorrocks, B., 1981. Competition on a divided and ephemeral resource: a simulation model. J. Anim. Ecol. 48, 91-102.

Baker, T. C., Vickers N. J., 1997. Pheromone-mediated flight in moths. In: Pheromone Research: New Directions. Cardé, R. T., Minks A. K. (eds.) Chapman and Hall, New York. pp. 248-264.

Bartelt, R.J., Schaner, A.M., Jackson, L.L., 1985. *cis*-vaccenyl acetate as an aggregation pheromone in *Drosophila melanogaster*. J. Chem. Ecol. 11(9), 1747-1756.

Bell, W.J., Cardé, R.T. (Eds.), 1984. *Chemical ecology of insects*. Chapman & Hall, London New York.

Bell, W.J., Cardé, R.T., 1995. Chemical Ecology of Insects, vol. 2. Chapman & Hall, London.

Bell, W.J., Kipp, L.R., Collins, R.D., 1995. The role of chemo-orientation in search behavior. In: Bell, W.J., Cardé, R.T. (Eds.), Chemical Ecology of Insects, vol. 2, pp. 105–152. Chapman & Hall, New York

Berec, L., Boukal, D.S., Berec, M., 2001. Linking the Allee effect, sexual reproduction, and temperature-dependent sex determination via spatial dynamics. Am. Nat. 157, 217-230.

Berec, L., Angulo, E., Courchamp, F., 2007. Multiple Allee effects and population management. Trends Ecol. Evol. 22(4), 185-191.

Boone, C.K., Six, D.I., Zheng, Y., Raffa, K.F., 2008. Parasitoids and dipteran predators exploit volatiles from microbial symbionts to locate bark beetles. Environ. Entomol. 37(1), 150-161.

Bouletreau, J., 1978. Ovarian activity and reproductive potential in a natural population of *Drosophila melanogaster*. Oecologia 35(3), 319–342.

Boulétreau-Merle, J., Fouillet, P., Varaldi, J., 2003. Divergent strategies in low temperature environment for the sibling species *Drosophila melanogaster* and *D. simulans*: overwintering in extension border areas of France and comparison with African populations. Evol. Ecol. 17(5–6), 523–548.

Brewster, C.C., Allen, J.C., 1997. Spatiotemporal model for studying insect dynamics in large-scale cropping systems. *Environ. Entomol.* 26, 473-482.

Bruce, T.J.A., Wadhams, L.J., Woodcock, C.M., 2005. Insect host location: A volatile situation. Trends Plant Sci 10, 269–274.

Bruinsma M., Dicke M., 2008. Herbivore-induced indirect defence: from induction mechanisms to communitie ecology. In: Schaller, A. (Ed.) Induced plant resistance to herbivory, Springer Science + Business Media, Berlin, pp 31-60.

Budick, S.A., Dickinson, M.H., 2006. Free-flight responses of *Drosophila melanogaster* to attractive odors. J. Exp. Biol. 209, 3001–3017.

Bukovinszky, T., Gols, R., Hemerik., L., van Lenteren, J.C., Vet, L.E.M., 2007. Time allocation of a parasitoid foraging in heterogeneous vegetation: implications for host-parasitoid interactions. J. Anim. Ecol. 76, 845-853.

Cardé, R.T., 1984. Chemo-orientation in flying insects. In: Bell, W.J., Cardé, R.T. (Eds.), Chemical Ecology of Insects, pp. 111–124. Chapman & Hall, London

Cardé R.T., Mafra-Neto , A., 1997. Mechanisms of flight of male moths to pheromone. In: Pheromone Research: New Directions. Cardé, R. T., Minks A. K. (eds.) Chapman and Hall, New York.

Cardé, R.T., Minks, K.A., 1997. Insect Pheromone Research, New Directions. Chapman & Hall, New York.

Charnov, E.L., 1976. Optimal foraging: the marginal value theorem. Theor. Pop. Biol. 9, 129-136.

Chow, D.M., Frye, M.A., 2009. The neuro-ecology of resource localization in Drosophila. Behavioral components of perception and search. Fly 3(1), 50-61.

Chow, D.M., Theobald, J.C., Frye, M.A., 2011. An olfactory circuit increases the fidelity of visual behavior. J. Neuroscience 31(42), 15035-15047.

De Boer, J.G., Dicke, M., 2004. Experience with methyl salicylate affects behavioural responses of a predatory mite to blends of herbivore-induced plant volatiles. Entomol. Exp. Appl. 110, 181-189.

De Gee, M., Lof, M.E., Hemerik, L., 2008. The effect of chemical information on the spatial distribution of fruit flies: II parameterization, calibration and sensitivity. Bull. Math. Biol. 70, 1850-1868.

De Moraes C.M., Lewis, W.J., Paré, P.W., Alborn, H.T., Tumlinson, J.H., 1998. Herbivore-infested plants selectively attract parasitoids. Nature, 393, 570-573.

Dicke, M., van Lenteren, J.C., Boskamp, G.J.F., van Dongen-van Leeuwen, E., 1984. Chemical stimuli in host-habitat location by *Leptopilina heterotoma* (Thomson) (Hymenoptera: Eucoilidae), a parasitoid of *Drosophila*. J. Chem. Ecol. 10, 695-712.

Dicke, M., Van Lenteren, J.C., Boskamp, G.J.F., Voorst, R. Van, 1985. Intensification and prolongation of host searching in *Leptopilina heterotoma* (Thomson) (Hymenoptera: Eucoilidae) through a kairomone produced by *Drosophila melanogaster*. J. Chem. Ecol. 11,125-136.

Dicke M., van Beek, T.A., Posthumus, M.A., Ben Dom, N., van Bokhoven, H., de Groot AE., 1990. Isolation and identification of volatile kairomone that affects acarine predator-prey interactions: involvement of host plant in its production. J. Chem. Ecol. 16, 381-396.

Dicke, M., Vet, L.E.M., Wiskerke, J.S.C., Stapel, O., 1994. Parasitoid of Drosophila larvae solves foraging problem through infochemical detour: conditions affecting employment of this strategy. Norwegian J. Agricultural Sciences, 16, 227-232.

Dicke, M., 1999. Are herbivore-induced plant volatiles reliable indicators of herbivore identity to foraging carnivorous arthropods? Entomol. Exp. Appl. 91, 131-142.

Dicke, M., Sabelis, M.W., 1988. Infochemical terminology: based on cost-benefit analysis rather than origin of compounds? Funct. Ecol. 2, 131-139.

Dicke, M., Grostal, P., 2001. Chemical detection of natural enemies by arthropods: an ecological perspective. Annu. Rev. Ecol. Syst. 32, 1-23.

Dicke, M., Takken, W. (Eds.), 2006. Chemical ecology: from gene to ecosystem. Springer, Dordrecht.

Dicke, M., Baldwin, I.T., 2010. The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry-for-help'. Trends Plant Sci. 15, 167-175.

Dormand, J. R., Prince, P. J., 1980. A family of embedded Runge-Kutta formulae. J. Comp. Appl. Math. 6 (1), 19-26.

Echeverria, G., Fuentes, M.T., Graell, J., Lopez, M.L., 2003. Relationships between volatile production, fruit quality and sensory evaluation of Fuji apples stored in different atmospheres by means of multivariate analysis. J. Sci. Food Agr. 84(1), 5–20.

Elkinton, J.S., Cardé, R.T., 1984. Odor dispersion. In: Bell, W.J., Cardé, R.T. (Eds.), Chemical Ecology of Insects, pp. 73–91. Chapman & Hall, London.

Etienne, R., Wertheim, B., Hemerik, L., Schneider, P., Powell, J., 2000. Dispersal may enable persistence of fruit flies suffering from the Allee effect and scramble competition. Proc. Exper. Appl. Entomol., Neth. Entomol. Soc. 11, 121–128.

Etienne, R., Wertheim, B., Hemerik, L., Schneider, P., Powell, J.A., 2002. The interaction between dispersal, the Allee effect and scramble competition affects population dynamics. Ecol. Model. 148(2), 153–168.

Farrell, J.A., Murlis, J., Long, X., Li,W., Cardé, R.T., 2002. Filament based atmospheric dispersion model to achieve short time-scale structure of odor plumes. Environ. Fluid Mech. 2(1–2), 143–169.

Fatouros, N.E., Huigens, M.E., van Loon, J.J.A., Dicke, M., Hilker, M., 2005a. Butterfly anti-aphrodisiac lures parasitic wasps. Nature, 433, 704.

Fatouros, N.E., van Loon, J.J.A., Hordijk, K.A., Smid, H.M., Dicke, M., 2005b. Herbivore induced plant volatiles mediate in-flight host discrimination by parasitoids. J. Chem. Ecol. 31, 2033-2047.

Fatouros, N.E., Dicke, M., Mumm, R., Meiners, T., Hilker, M., 2008. Foraging behavior of egg parasitoids exploiting chemical information. Behav. Ecol. 19, 677-689.

Fleury, F., Ris, N., Allemand, R., Fouillet, P., Carton, Y., Boulétreau, M., 2004. Ecological and genetic interactions in *Drosophila*-parasitoids communities: a case study with *D. melanogaster*, *D. simulans* and their common *Leptopilina* parasitoids in south-eastern France. Genetica, 120, 181-194.

Fraker, M.E., 2008. The dynamics of predation risk assessment: responses of anuran larvae to chemical cues of predators. J. Anim. Ecol. 77, 638-645.

Frye, M.A., Tarsitano, M., Dickinson, M.H., 2003. Odor localization requires visual feedback during free flight in *Drosophila melanogaster*. J. Exp. Biol. 206(5), 843–855.

Godfray, H.C.J., 1994. Parasitoids: behavioral and evolutionary ecology. Princeton University Press, Princeton, NJ.

Gilbert, C., Robertson, G., Le Maho, Y, Naito, Y., Ancel, A., 2006. Huddling behavior in emperor penguins : Dynamics of huddling. Physiol. Behav. 88, 479-488.

Haccou, P., de Vlas, S.J., van Alphen, J.J.M., Visser, M.E., 1991. Information processing by foragers: effects of intra-patch experience on the leaving tendency of *Leptopilina heterotoma*. J. Anim. Ecol. 60, 93-106.

Hamilton, W.D., 1971. Geometry for the selfish herd. J.Theor. Biol. 31, 295-311.

Hare, J.D., 2011. Ecological Role of Volatiles Produced by Plants in Response to Damage by Herbivorous Insects. Annu. Rev. Entomol. 56, 161-180.

Hassell, M.P., 2000. The spatial and temporal dynamics of host-parasitoid interactions. Oxford University Press, Oxford.

Hedlund, K., Vet, L.E.M., Dicke, M., 1996. Generalist and specialist parasitoid strategies of using odours of adult drosophilid flies when searching for larval hosts. Oikos, 77, 390-398.

Heil, M., 2008. Indirect defence via tritrophic interactions. New Phytol. 178, 41-61.

Hirzel, A.H., Nisbet, R.M., Murdoch, W.W., 2007. Host-parasitoid spatial dynamics in heterogeneous landscapes. Oikos 116, 2082-2096.

Hoffmeister, T.S., Rohlfs, M., 2001. Aggregative egg distributions may promote species co-existence—but why do they exist? Evol. Ecol. Res. 3(1), 37–50.

Holling, C.S., 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canad. Entomol. 91, 293-320.

Hutner, S.H., Kaplan, H.M., Enzmann, E.V., 1937. Chemicals attracting *Drosophila*. Am. Nat. 71(737), 575-581.

Ives, A.R., 1992. Continuous-time models of host-parasitoid interactions. Am. Nat. 140(1), 1-29.

Janssen, A., Driessen, G., de Haan, M., Roodbol, N., 1988. The impact of parasitoids on natural populations of temperate woodland *Drosophila*. Neth. J. Zool. 38(1), 61-73.

Kats, L.B., Dill, L.M., 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Ecoscience 5, 261-394.

Keller, E.F., Segel, L.A., 1971. Model for chemotaxis. J. Theor. Biol. 30, 225-234

Kellogg, F.E., Frizel, D.E., Wright, R.H., 1962. The Olfactory Guidance of Flying Insects. IV. Drosohila. Can. Entomol. 94(8), 884–888.

Kennedy, J. S., 1940. The visual responses of flying mosquitoes. Proc. Zool. Soc. Lond. Ser. A 109, 221-242.

Kennedy, J. S., Marsh, D., 1974. Pheromone-regulated anemotaxis in flying moths. Science 184, 999-1001.

Kolss, M., Hoffmeister, T.S., Hemerik, L., 2006. The theoretical value of encounters with parasitized hosts for parasitoids. Behave. Ecol. Sociobiol. 61, 291-304.

Kowaldo, G., Russell, R. A., 2008. Robot odor localization: A taxonomy and survey. Int. J. Robotics Research 27(8), 869–894.

Krebs, J.R., Davies, N.B. (Eds.), 1997. Behavioural ecology: an evolutionary approach. 4th Edition. Blackwell Science Ltd., Oxford.

Krijger, C.L., Sevenster, J.G., 2001. Higher species diversity explained by stronger spatial aggregation across six neotropical *Drosophila* communities. Ecol. Let. 4, 106-115.

Lof, M.E., Etienne, R.S., Powell, J., De Gee, M., Hemerik, L., 2008. The effect of chemical information on the spatial distribution of fruit flies: I model results. Bull. Math. Biol. 70, 1827-1849.

Lo Iacono, G., 2010. A comparison of different searching strategies to locate sources of odor in turbulent flows. Adapt. Behav. 18, 155-170.

Lotka, A.J., 1925. Elements of physical biology. Wiliams and Wilkins, Baltimore.

Monod, J., 1949. The growth of bacterial cultures. Annu. Rev. Microbiol. 3, 371-394.

Morais, P.B., Martins, M.B., Klaczko, L.B., Mendonça-Hagler, L.C., Hagler, A.N., 1995. Yeast succession in the amazon fruit *Parahancornia amapa* as resource partitioning among *Drosophila* spp. Appl. Environ. Microbiol. 61(12), 4251-4257.

Murlis, J., Elkington, J.S., Cardé, R.T., 1992. Odor plumes and how insects use them. Annu. Rev. Entomol. 37, 505–532.

Neubert, M.G., Kot, M., Lewis, M.A., 1995. Dispersal and pattern formation in a discrete-time predator-prey model. Theor. Popul. Biol. 48(1), 7–43.

Nguyen-Huu, T., Let, C., Poggiale, J.C., Auger, P., 2006. Effect ofmovement frequency on global host-parasitoid spatial dynamics with unstable local dynamics. Ecol. Model. 197, 290-295.

Nicholson, A.J., 1933. The balance of animal populations. J. Anim. Ecol. 2, 131-178.

Noldus, L.P.J.J., 1989. Chemical espionage by parasitic wasps : how Trichogramma species exploit moth sex pheromone systems. PhD thesis, Wageningen Agricultural University, Wageningen.

Noldus, L.P.J.J., van Lenteren, J.C., Lewis, W.J., 1991. How Trichogramma parasitoids use moth sex pheromone as kairomone: orientation behaviour in a wind tunnel. Physiol. Entomol. 16, 313-327.

Ostränd, F., Anderbrant, O., 2003. From where are insects recruited? A new model to interpret catches of attractive traps. Agr. Forest Entomol. 5, 163-171.

Papaj, D.R., Vet, L.E.M., 1990. Odor learning and foraging success in the parasitoid, *Leptopilina heterotoma*. J. Chem. Ecol. 16 (11), 3137-3150.

Parrish, J.K., Edelstein-Keshet, L., 1999. Complexity, pattern, and evolutionary trade-offs in animal aggregation. Science 284 (#5411), 99-101.

Pearce, I.G., Chaplain, M.A.J., Schofield, P.G., Anderson, A.R.A., Hubbard, S.F., 2006. Modelling the spatio-temporal dynamics of multi-species host-parasitoid interactions: heterogeneous patterns and ecological implications. J. Theor. Biol. 241, 876-886.

Pearce, I.G., Chaplain, M.A.J., Schofield, P.G., Anderson, A.R.A., Hubbard, S.F., 2007. Chemotaxis-induced spatio-temporal heterogeneity in multi-species host-parasitoid systems. J. Math. Biol. 55, 365-388.

Poelman, E.H., van Loon, J.J.A., Dicke, M., 2008. Consequences of variation in plant defense for biodiversity at higher trophic levels. Trends Plant Sci. 13 (11), 534-541.

Postma, M., 2003. Spatial and temporal aspects in biological signal transduction: diffusion, reaction and geometry in *Drosophila* phototransduction and *Dictyostelium* chemotaxis. PhD thesis, University of Groningen, Groningen, The Netherlands.

Powell, J.A., McMillen, T., White, P., 1998. Connecting a chemotactic model for mass attack to a rapid integro-difference emulation strategy. SIAM J. Appl. Math. 59(2), 547–572.

Powell, J.A., 2002. Spatio-temporal models in ecology; an introduction to integro-difference equations. http://www.math.utah.edu/adler/minicourse-/matlab/labs_powell.pdf.

Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N., Weis, A.E., 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Annu. Rev. Ecol. Syst. 11, 41–65

Puente, M., Magori, K., Kennedy, G.G., Gould, F., 2008. Impact of herbivore-induced plant volatiles on parasitoid foraging success: a spatial simulation of the *Cotesia rubecula*, *Pieris rapae*, and *Brassica oleracea* system. J. Chem. Ecol. 34, 959-970.

Raffa, K.F., 2001. Mixed messages across multiple trophic levels: the ecology of the bark beetle chemical communication systems. Chemoecology 11, 49-65.

Raffa, K.F., Hobson, K.R., LaFontaine, S., Aukema, B.H., 2007. Can chemical communication be cryptic? Adaptations by herbivores to natural enemies exploiting prey semiochemistry. Oecologia 153, 1009-1019.

Robinet, C., Lance, D.R., Thorpe, K.W., Onufrieva, K.S., Tobin, P.C., Liebhold, A.M., 2008. Dispersion in time and space affect mating success and Allee effects in invading gypsy moth populations. J. Anim. Ecol. 77, 966-973.

Rohlfs, M., Hoffmeister, T.S., 2003. An evolutionary explanation of the aggregation model of species coexistence. Proc. R. Soc. Lond. B (Suppl.) 270, S33–S35.

Rohlfs, M., Hoffmeister, T.S., 2004. Spatial aggregation across ephemeral resource patches in insect communities: an adaptive response to natural enemies? Oecologia 140(4), 654–661.

Rohlfs, M., Hoffmeister, T.S., 2005. Maternal effects increase survival probability in *Drosophila subobscura* larvae. Entomol. Exp. Appl. 117(1):51-58.

Rohlfs, M., Obmann, B., Petersen, R., 2005. Competition with filamentous fungi and its implication for a gregarious lifestyle in insects living on ephemeral resources. Ecol. Entomol. 30(5), 556-563.

Rohlfs, M., 2006. Genetic variation and the role of insect life history traits in the ability of *Drosophila* larvae to develop in the presence of a competing filamentous fungus. Evol. Ecol. 20 (3), 271-289.

Rohlfs, M., 2008. Host-parasitoid interaction as affected by interkingdom competition. Oecologia 155(1), 161-168.

Sabelis, M.W., Schippers, P., 1984. Variable wind directions and anemotactic strategies of searching for an odour plume. Oecologia 63, 225-228.

Sang, J.H., 1956. The quantitative nutritional requirements of *Drosophila melanogaster*. J. Exp. Biol. 33(1), 45–72.

Schaner, A.M., Bartelt, R.J., Jackson, L.L., 1987. (Z)-11-octadecenyl acetate, an aggregation pheromone in *Drosophila simulans*. J. Chem. Ecol. 7, 1777–1786.

Schoonhoven, L.M., van Loon, J.J.A., Dicke, M., 2005. Insect-Plant Biology, 2nd edn. Oxford University Press, London.

Schofield, P.G., Chaplain, M.A.J., Hubbard, S.F., 2002. Mathematical modelling of host-parasitoid systems: effects of chemically mediated parasitoid foraging strategies on within- and between-generation spatio-temporal dynamics. J. Theor. Biol. 214, 31-47.

Schofield, P.G., Chaplain, M.A.J., Hubbard, S.F., 2005. Dynamic heterogeneous spatio-temporal pattern formation in host-parasitoid systems with synchronized generations. J. Math. Biol. 50, 559-583.

Shorrocks, B., Sevenster, J.G., 1995. Explaining local species diversity. Proc. Royal. Soc. London Series B. 260, 305-309.

Shea, P.J., McGregor, M.D., Daterman, G.E., 1992. Aerial application of verbenone reduces attack of lodgepole pine by mountain pine beetle. Can. J. Forest. Res. 22(4), 436–441.

Shiojiri, K., Takabayashi, J., Yano, S, Takafuji, A., 2001. Infochemical mediated tritrophic interaction webs on cabbage plants. Pop. Ecol. 43, 23-29.

Sokal, R.R., Rohlf, F.J., 1981. Biometry, 2nd edn. W.H. Freeman and Company, New York.

Southwood, T.R.E., Henderson, P.A., 2000. Ecological Methods, 3rd edn. Blackwell Science Ltd, Oxford.

Stephens, P.A., Sutherland, W.J., Freckleton, R.P., 1999. What is the Allee effect? Oikos 87(1), 185-190.

Stewart, F.J., Baker, D.A., Webb, B., 2010. A model of visual-olfactory integration for odour localisation in free-flying fruit flies. J. Exp. Biol. 213, 1886-1900.

Sutton, O.G., 1953. Micrometeorology. McGraw–Hill, New York.

Symonds, M.R.E., Wertheim, B., 2005. The mode of evolution of aggregation pheromones in Drosophila species. J. Evol. Biol., 18, 1253-1263.

Takabayashi, J., Takahashi, S., Dicke, M., Posthumus, M.A., 1995. Developmental stage of herbivore *Pseudaletia separata* affects production of herbivore-induced synomone by corn plants. J. Chem. Ecol. 21, 273-287.

Tammero, L.F., Dickinson, M H., 2002. The influence of visual landscape on the free flight behavior of the fruit fly *Drosophila melanogaster*. J. Exp. Biol. 205, 327-343.

Taylor, C.M., Hastings, A., 2005. Allee effects in biological invasions. Ecol. Let. 8, 895-908.

Tentelier, C., Fauvergue, X., 2007. Herbivore-induced plant volatiles as cues for habitat assessment by a foraging parasitoid. J. Anim. Ecol. 76, 1-8

Thompson, W.R., 1930. The utility of mathematical methods in relation to work on biological control. Ann. Appl. Biol. 17, 641-648.

Tilman, D., Kareiva, P. (Eds.), 1997. Spatial Ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, NJ.

Timofeeff-Ressovsky, N.W., Timofeeff-Ressovsky, E.A., 1941. Populationgenetische Versuche an *Drosophila* II. Aktionsbereiche von *Drosophila funebris* und *Drosophila melanogaster*. Z. Induct. Abstamm. Ver. 79, 35–43.

Turchin, P., 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates Inc., Sunderland, Massachusetts.

Turlings, T.C.J., Tumlinson, J.H., Lewis, W.J., 1990. Exploitation of herbivore-induced plant odors by host-seeking parasiticwasps. Science, 250, 1251–1253.

Turlings, T.C.J., Loughrin, J.H., McCall, P.J., Rose, U.S.R., Lewis, W.J., Tumlinson, J.H., 1995. How caterpillar-damaged plants protect themselves by attracting parasitic wasps. PNAS 92, 4169-4174.

Turlings, T.C.J., Wäckers, F.L., 2004. Recruitment of predators and parasitoids by herbivore-injured plants. In: Cardé, R.T., Millar, J. (Eds.). Advances in chemical ecology of insects, pp 21-75.

Varaldi, J., Fouillet, P., Boulétreau, M., Fleury, F., 2005. Superparasitism acceptance and patch-leaving mechanisms in parasitoids: a comparison between two sympatric wasps. Anim. Behav. 69, 1227-1234.

Varley, G.C., 1947. The natural control of population balance in the knapweed gallfly (*Urophora jaceana*). J. Anim. Ecol. 16, 139-187.

Van Lenteren, J.C., Bakker, K., 1978. Behavioural aspects of the functional responses of a parasitoid (*Pseudeucoila bochei* Weld) to its host (*Drosophila melanogaster*). Neth. J. Zool. 28, 213-233.

Van Loon, J.J.A., de Boer, J.G., Dicke, M., 2000. Parasitoid–plant mutualism, parasitoid attack of herbivore increases plant reproduction. Entomol. Exp. Appl. 97, 219–227.

Vet, L.E.M., Dicke, M., 1992. Ecology of infochemical use by natural enemies in a tritrophic context. Annu. Rev. Entomol. 37, 141-172.

Vet, L.E.M., Groenewold, A.W., 1990. Semiochemicals and learning in parasitoids. J. Chem. Ecol. 16, 3119-3135.

Vet, L.E.M., 1999. From chemical to population ecology: infochemical use in an evolutionary context. J. Chem. Ecol. 25, 31-49.

Vickers, N. J., 2000. Mechanisms of animal navigation in odor plumes. Biol. Bull. 198 (2), 203-212.

Volterra, V., 1931. Variations and fluctuations of the number of individuals in animal species living together. In: Animal Ecology, Chapman, R.N. (ed), McGraw-Hill.

Vos, M., Vet, L.E.M., Wäkers, F.L., Middelburg, J.J., van der Putten, W.H., Mooij, W.M., Heip, C.H.R., van Donk, E., 2006. Infochemicals structure marine, terrestrial and freshwater food webs: implications for ecological informatics. Ecol. Inform. 1, 23-32.

Wajnberg, E., Bernstein E., van Alphen, J.M. (Eds.), 2008. Behavioral ecology of insect parasitoids. From theoretical approaches to field applications. Blackwell Publishing Ltd, Oxford.

Wall, C., Perry, J.N., 1987. Range of action of moth sex-attractant sources. Entomol. Exp. Appl.44, 5–14.

Weissburg, M.J., Dusenbery, D.B., Ishida, H., Janata, J., Keller, T., Roberts, P.J.W., Webster, D.R., 2002. A multidisciplinary study of spatial and temporal scales containing information in turbulent chemical plume tracking. Environ. Fluid. Mechan. 2, 65-94.

Wertheim, B., 2001. Individual risk of parasitism in host aggregations: A behaviour-based model on functional and numerical responses. In: Ecology of *Drosophila* aggregation pheromone: a multitrophic approach. pp. 111-138. PhD Thesis, Wageningen University, Wageningen, The Netherlands.

Wertheim, B., 2001. Ecology of *Drosophila* aggregation pheromone: a multitrophic approach. PhD Thesis, Wageningen University, Wageningen, The Netherlands

Wertheim, B., Dicke, M., Vet, L.E.M., 2002a. Behavioral plasticity in support of a benefit for aggregation pheromone use in *Drosophila melanogaster*. Entomol. Exp. Appl. 103(1), 61–71.

Wertheim, B., Marchais, J., Vet, L.E.M., Dicke, M., 2002b. Allee effect in resource exploitation in *Drosophila*: an interaction among density of adults, larvae, and micro-organisms. Ecol. Entomol. 27, 608-617.

Wertheim, B., Vet, L.E.M., Dicke, M., 2003. Increased risk of parasitism as ecological costs of using aggregation pheromones: laboratory and field study of *Drosophila-Leptopilina* interaction. Oikos, 100(2), 269-282.

Wertheim, B., van Baalen, E-J., A., Dicke, M., Vet, L.E.M., 2005. Pheromone-mediated aggregation in nonsocial arthropods: an evolutionary ecological perspective. Annu. Rev. Entomol. 50, 321-346.

Wertheim, B., Allemand, R, Vet, L.E.M., Dicke, M., 2006. Effects of aggregation pheromone on individual behaviour and food web interactions: a field study on *Drosophila*. Ecol. Entomol. 31(3), 216-226.

West, A.S., 1961. Chemical attractants for adult *Drosophila* species. J. Econom. Entomol. 54 (4), 676-681.

Wiskerke, J.S.C., Dicke, M., Vet, L.E.M., 1993. Larval parasitoid uses aggregation pheromone of adult hosts in foraging behaviour: a solution to the reliability-detectability problem. Oecologia, 93(1), 145-148.

Wyatt, T.D., 2004. Breaking the code: illicit signallers and receivers of semiochemical signals. In: Pheromones and animal behaviour: communication by smell and taste. Cambridge University Press, Cambridge, pp. 229-250.

Yamanaka, T., Tatsuki, S., Shimada, M., 2003. An individual-based model for sex-pheromone-oriented flight patterns of male moths in a local area. Ecol. Model. 161(1–2), 35–51.

Yin,Y., Chen, N., Zhang1, S., Guo1, A., 2010. Choice strategies in Drosophila are based on competition between olfactory memories. Europ. J. Neuroscience 30, 279–288.

Summary

Many species ranging from microbes to mammals use chemicals to communicate. These chemicals, called infochemicals, can provide information on the availability of food or mates, as well as the presence of competitors or natural enemies. Therefore, they can affect interactions between species in a food web. Once an infochemical is emitted, in principle any organism can exploit its information. Infochemicals affect the dispersal and distribution of organisms, the distribution of competitor species and natural enemies, and consequently, the population dynamics of many food web species. Yet, the study of chemical information use has been mostly restricted to studies at the level of individual organisms and the identification of chemical substances that convey the information. The central question in this thesis is how chemical information conveyance affects spatial population dynamics of species and the interactions between species within a food chain. To answer this question, a modelling approach has been used. By using simulation models, one can study the effect of changing parameters that are difficult to estimate by direct experiments, while at the same time keeping other factors constant. In this study, different responses (or no response at all) to chemical information by the host and its parasitoid have been artificially established. The model system that I used consists of the fruit fly *Drosophila melanogaster*, and its natural enemy, the parasitoid *Leptopilina heterotoma*. *D. melanogaster* uses its aggregation pheromone in combination with odours from fermenting fruit to localize suitable resources for reproduction. *L. heterotoma* uses these same odours to localize its host, the larvae of the fruit fly.

For *D. melanogaster*, aggregation on a resource can be beneficial when a population is small and has to overcome negative effects associated with low population densities. Such negative effects, known as the Allee effect, can for instance be caused by difficulties in finding a mate or by difficulties in resource exploitation. However, aggregation also involves costs, because individuals within an aggregation frequently experience more severe competition for food, space and mates than they would experience when being on their own. This leads to the question: why does a host species use an aggregation pheromone when aggregating can result in increased competition and the communication system used to aggregate can be spied upon by a natural enemy? In this thesis, I examine the effects of infochemical use by the fruit flies on its population dynamics in the absence of natural enemies (**Chapter 2-4 & 6**). **Chapter 5** addresses the effect of the use of aggregation pheromones on the population dynamics of the fruit fly in the presence of parasitoids that are capable of exploiting their communication system.

The effect of chemical information on population dynamics

Chapter 2 presents a mathematical spatial-temporal model for fruit fly behaviour. It describes the development in time of the averaged whereabouts (local densities) of a fruit fly population in an orchard. The fruit flies are divided into three subpopulations according to their activity state: exploiting a resource, leaving their old resource, or searching for a new resource, respectively. The model also incorporates the time-dependent odour distribution in the orchard, and the fruit fly responses thereupon. This model is used to run numerical simulations, with a total length of one season. As the season contains about ten generations, the simulation results enabled to study the fruit fly population dynamics at the scale of one year, and the role of infochemicals on the population size. When the fruit fly population was small, the use of infochemicals had a positive effect on population growth. When fruit flies could use chemical information, the settlement of adult fruit flies was higher, which reduced the local larval mortality due to the Allee effect. This positive effect outweighed the negative effect of increased mortality due to competition. However, when the whole area was colonized and the population was large, competition negatively affected population size. In this situation, the fruit fly population was larger when they could not use chemical information to aggregate on the resources.

Chapter 3 explains the role of the parameters in the model. Here, the values of the parameters are connected to results in the literature where possible. Furthermore, a sensitivity analysis is presented that shows to what extent the simulation results depend on the chosen parameter values.

Aggregation enhances colonization ability fruit flies

In Chapter 2, the initial fruit fly population was situated in the centre of the orchard. In reality, fruit flies hibernate outside the breeding area. At the beginning of the season they have to re-colonize the breeding area from the boundaries. **Chapter 4** uses the same model as used in Chapter 2, but now situated the initial population outside the orchard. The results show that, when fruit flies have to re-colonize the area from outside, the use of chemical information was crucial for the colonization of the area. The model results show that, under plausible assumptions, a randomly dispersing population – that could not use chemical information – was not able to colonize the area that contained the apples. When an Allee effect on larval survival existed, the randomly dispersing population went extinct. However, the results indicate that even without an Allee effect, the randomly dispersing population could not colonize the orchard successfully. This indicates that for fruit flies it is essential to use chemical information – especially that from the aggregation pheromone – when colonizing an area.

Allee effect on larval development

The results from this modelling study indicate that the use of chemical information is especially useful when the population is small, mainly because aggregation by the adult fruit flies reduced the local mortality due to the Allee effect in their larvae (**Chapters 2** and **4**). In *D. melanogaster*, several mechanisms have previously been shown to contribute to an Allee effect. Firstly, adult aggregation has a positive effect on larval survival because adults alter the suitability of the resource for the juveniles. Adults, especially females, vector a diversity of yeasts and inoculate the resource with these yeasts during their presence. As fruit fly larvae feed on yeast, inoculation of the resource with yeast improves the habitat for the larvae. Secondly, this increase in yeast also reduces fungal growth. This positively affects larval survival, because the fungi can cause a high mortality in fruit fly larvae. Thirdly, the larvae of *D. melanogaster* themselves are also able to suppress fungal growth by disrupting the hyphae of the fungus. Larger groups of larvae are more successful at this than smaller groups.

Spying enemies affect fruit fly population dynamics

Most studies on the effect of infochemicals focus on plant-herbivore-parasitoid or predator interactions. In these studies the natural enemy often uses herbivore-induced plant volatiles to locate its host or prey. **Chapter 5** addresses how chemical information affects the interaction between hosts and parasitoids in a system where a parasitoid spies on the intraspecific communication of its host. For this purpose, the spatio-temporal model developed in Chapter 2 has been extended with the population dynamics of the parasitoid and the interaction between the parasitoid and the host. The exploitation of chemical information by the parasitoid appeared to negatively affect the size and growth of the fruit fly population. Moreover, when parasitoids exploited chemical information, the average parasitism rate was higher. As a result, the population growth rate of the fruit flies was lower. Therefore, it took longer to overcome the negative effects associated with a small population size – the Allee effect. Furthermore, this negative effect was stronger when fruit flies were not able to use chemical information and had to find the resources by random dispersal.

A diluted risk of predation or parasitism is considered as one of the possible advantages of aggregation. However, the simulations did not provide evidence for a locally diluted risk of parasitism at higher larval densities. In contrast, the simulations showed that larval mortality due to parasitism increased with larval density on a resource.

The simulations showed no difference in fruit fly population size and larval mortality due to parasitism, between situations where parasitoids exploited the aggregation pheromone of the fruit fly adults and those where the parasitoids could only respond to chemicals emitted by the host habitat. These results indicate that for *D. melanogaster* there is no additional cost, with respect to an increased risk of parasitism, for the use of aggregation pheromone. Moreover, the use of chemical information by the host enhanced its population growth and enabled it to survive, even at higher parasitoid densities. Consistent with the outcomes of experimental studies, the simulations reported in this thesis showed that in the short term the presence of aggregation pheromone positively affects the localization of the resources by the parasitoids. However, in the long term, this stronger attraction does not result in higher parasitism than when they could only respond to food odours. The patch residence time of *L. heterotoma* is positively related to the number of hosts present on the patch. When the fruit fly population is large, the larval densities on the resources are high, and *L. heterotoma* spends a long time foraging. The simulations indicate that in that case arrestment on the resources is more important than the rate of finding a resource.

Odour discrimination and finding the most suitable source

Odour plume structure and resulting orientation behaviour have been studied in great detail in moths. However, in these studies only one odour source was present. In the case of the fruit fly, multiple resources are present that moreover differ in suitability for reproduction. In **Chapter 6**, individual based modelling is used to explore which set of behavioural rules can best describe the movement of a fruit fly towards an odour source, and what kind of behaviour is needed to be able to discriminate between odours that indicate different levels of resource suitability for reproduction. Here, a mathematical technique was used that is fundamentally different from the one used in **Chapters 2-5**. In **Chapters 2-5** partial differential equations and integro-differential equations for the expected local fruit fly (and parasitoid) density were numerically solved; this is the so-called mean-field approximation. In **Chapter 6**, a stochastic individual-based model was used to simulate the behaviour of several hundreds of fruit fly individuals directly. Because of the random effects, these simulations had to be repeated many times in order to distil the average pattern.

Behavioural decisions of moths appeared to be usable for odour tracking of fruit flies in a filamentous odour plume. However, these rules were not sufficient to guide the fruit flies to the most suitable odour source. In addition, fruit flies need to have a preference for the presence of both aggregation pheromones and food odours, “F+A”, over food odours in the absence of aggregation pheromone, “F”, to be able to distinguish between odour sources. However, this stronger preference does not have to be innate. As long as fruit flies are able to remember and adjust their current preference of “F+A” over “F” based on the odour concentrations of food odours and aggregation pheromone that they perceive, more fruit flies find the more attractive odour source. This is also what one would expect, because odour sources that only contain food odours are potentially suitable for reproduction. In an environment where no aggregation pheromone is present yet, all fruit flies are attracted to only food odours and have opportunities to meet other individuals there. Only from the moment that odour sources start emitting aggregation pheromone – an indication that other fruit flies are or have been laying eggs – these “F+A” sources become the more suitable odour sources.

Furthermore, this study shows that including downwind flight when a fruit fly loses contact with the odour plume, and does not find the plume back again within 3 casts, greatly enhanced the number of fruit flies that found the “F+A” odour sources.

The outcome of the models was compared with experimental data of Wertheim et al. (2002a). The models developed show good potential for estimating how many fruit flies settle down on the “F+A” and “F” sources. However, they were not able to predict the spatial distribution of the fruit flies over the different odour sources correctly yet.

General conclusion

This thesis shows that the use of chemical information by a host – *D. melanogaster* - affects its population dynamics. In the absence of a natural enemy, and when the host population is small, the use of chemical information has a positive effect on population growth and enhances the fruit fly’s colonization ability. But when the population becomes larger, the negative effects of larval competition are stronger than the positive effects of reduced mortality due to the Allee effect. However, the use of chemical information was crucial to colonize an area from the boundaries. A fruit fly population that was unable to use chemical information could not colonize the area and went extinct. When parasitoids can use chemical information, parasitism rates were higher, resulting in a slower population growth of their host. Yet, the use of chemical information also influenced the interaction between the parasitoid and the host. The use of chemical information by the host enhanced its population growth in the presence of the parasitoid and enabled persistence of the fruit fly population even at higher parasitoid densities.

Samenvatting

Veel soorten, van microben tot zoogdieren, gebruiken chemische stoffen (geur- en smaakstoffen) als communicatiemiddel. Deze chemische stoffen worden informatiestoffen genoemd. Zij kunnen informatie verschaffen over de beschikbaarheid van voedsel en potentiële partners, maar ook over de aanwezigheid van concurrenten of natuurlijke vijanden. Daardoor kunnen ze de interacties tussen soorten in een voedselweb beïnvloeden. Vanaf het moment dat een geurstof uitgezonden is, kan in principe elk organisme de informatie die het bevat uitbuiten. Informatiestoffen hebben daardoor invloed op de verspreiding (in ruimte en tijd) van organismen, op de verspreiding van hun concurrenten en natuurlijke vijanden, en daardoor op de populatiedynamica van de soorten in een voedselweb. Toch is het onderzoek naar het gebruik van informatiestoffen meestal beperkt tot het niveau van individuele organismen en de identificatie van de chemische stoffen die de informatie overdragen. De centrale vraag in dit proefschrift is hoe de overdracht van informatie door chemische stoffen de ruimtelijke populatiedynamiek van een soort beïnvloedt, en de interactie tussen soorten in een voedselketen. Om deze vraag te beantwoorden is gebruik gemaakt van wiskundige modellen. Door middel van simulatiemodellen kunnen we onderzoeken wat er gebeurt als we parameters veranderen die moeilijk te schatten zijn in directe experimenten, terwijl we andere factoren gelijk houden. In dit onderzoek zijn verschillende typen respons (of helemaal geen respons) op informatiestoffen van een gastheer en een natuurlijke vijand bestudeerd. Het modelsysteem dat ik gebruik bestaat uit de fruitvlieg *Drosophila melanogaster*, en zijn natuurlijke vijand, de sluipwesp *Leptopilina heterotoma.* Een sluipwesp is een parasitoied, waarvan de vrouwtjes eitjes leggen op of in de gastheren (vaak eitjes of larven van andere insectensoorten). Terwijl de gastheer nog leeft ontwikkelt in het geval van *L. heterotoma* één sluipwespeitje per gastheer zich tot volwassen sluipwesp ten koste van de gastheer; de gastheer gaat uiteindelijke dood en er ontwikkelt zich dus geen volwassen individu van de gastheer. *D. melanogaster* gebruikt een vluchtig aggregatieferomoon (een vluchtige chemische stof met de eigenschap dat het soortgenoten aantrekt) in combinatie met geuren van gistend fruit om een geschikte locatie voor reproductie te vinden. *L. heterotoma* gebruikt diezelfde geuren om haar gastheer, de larven van de fruitvlieg, te localiseren.

Voor *D. melanogaster* kan het aggregeren (samenkomen) op een geschikte locatie voor reproductie voordelig zijn wanneer de fruitvliegpopulatie klein is, en er negatieve effecten die samenhangen met een lage populatiedichtheid overwonnen moeten worden. Deze negatieve effecten staan samen bekend als het Allee effect; zij kunnen bijvoorbeeld veroorzaakt worden door moeilijkheden bij het vinden van een partner, of door problemen bij het exploiteren van een voedselbron. Anderzijds zijn er ook kosten verbonden aan aggregeren. Bijvoorbeeld, individuen ervaren binnen een aggregatie vaak meer concurrentie om voedsel, ruimte en partners dan wanneer ze alleen zijn. Dit leidt tot de vraag: waarom gebruikt een soort een aggregatieferomoon wanneer aggregatie kan leiden tot een verhoogde concurrentie, terwijl bovendien het communicatiesysteem bespioneerd kan worden door een natuurlijke vijand? In dit proefschrift beschrijf ik mijn onderzoek naar het effect van het gebruik van informatiestoffen door de fruitvlieg op de populatiedynamica van de fruitvlieg in afwezigheid van een natuurlijke vijand (**Hoofdstuk 2-4 & 6**). **Hoofdstuk 5** betreft het effect van het gebruik van aggregatieferomoon op de populatiedynamica van de fruitvlieg in aanwezigheid van sluipwespen die het communicatiesysteem van de fruitvlieg kunnen gebruiken om hun gastheer te vinden.

Het effect van informatiestoffen op populatiedynamica

In **Hoofdstuk 2** wordt een wiskundig model gepresenteerd voor fruitvlieggedrag als functie van plaats en tijd. Dit model beschrijft hoe de verdeling (lokale dichtheid) van een fruitvliegenpopulatie in een boomgaard zich ontwikkelt in de loop van tijd. De fruitvliegen zijn verdeeld in drie subpopulaties, gebaseerd op hun activiteit op dat moment. We onderscheiden het verblijf op een gistende appel (bijvoorbeeld om te eten, te paren en eitjes te leggen), het vertrek vanaf een gistende appel, en het zoeken naar een nieuwe gistende appel. In het model is ook de tijdsafhankelijke geurverspreiding in de boomgaard opgenomen, en de reactie van de vliegen hierop. Met behulp van dit model zijn numerieke simulaties gedaan, met de tijdsduur van 10 generaties. De resultaten van de simulatie stelden ons in staat om de dynamica van de fruitvliegpopulatie en de invloed van informatiestoffen op de populatiegrootte te bestuderen, op de tijdschaal van een jaar. Wanneer de fruitvliegpopulatie klein was had het gebruik van informatiestoffen een positief effect op de populatiegroei. Wanneer fruitvliegen informatiestoffen konden gebruiken, vonden meer fruitvliegen een geschikte locatie voor reproductie, en dit verlaagde de lokale sterfte die werd veroorzaakt door het Allee effect. Echter, wanneer het hele gebied gekoloniseerd was en de populatie groot was, dan had concurrentie een negatief effect op populatiegrootte. In deze situatie was de fruitvliegpopulatie groter als ze niet gebruik konden maken van informatiestoffen.

Hoofdstuk 3 verklaart de rol van de verschillende parameters in het model. In dit hoofdstuk worden de parameterwaarden waar mogelijk gekoppeld aan resultaten uit de literatuur. Verder wordt een gevoeligheidsanalyse gepresenteerd die laat zien in hoeverre de simulatieresultaten afhankelijk zijn van de gekozen parameterwaarden.

Aggregatie verbetert het vermogen tot koloniseren van de fruitvlieg

In Hoofdstuk 2 begon de fruitvliegpopulatie in het midden van de boomgaard. In de werkelijkheid overwinteren fruitvliegen buiten de boomgaard. Aan het begin van het seizoen moeten ze dus het broedgebied vanaf de randen herkoloniseren. **Hoofdstuk 4** gebruikt hetzelfde model als in Hoofdstuk 2, alleen start de fruitvliegpopulatie buiten de boomgaard. De resultaten laten zien dat, onder geloofwaardige aannames, een populatie die geen geuren waarneemt (en alleen maar willekeurig kan zoeken) niet in staat was om de appels in de boomgaard te koloniseren. Wanneer er een Allee effect was op de overleving van de larven stierf de zich willekeurig verspreidende populatie uit. Echter, de resultaten van de simulaties zonder een Allee effect laten zien dat, zelfs zonder dit negatieve effect op kleine populaties, de random verspreidende populatie niet in staat was om het gebied succesvol te koloniseren. Dit wijst uit dat het gebruik van informatiestoffen – in het bijzonder het aggregatieferomoon – essentieel is om een gebied te koloniseren.

Allee effect op de ontwikkeling van de larven

De resultaten van deze modelstudie geven aan dat het gebruik van informatiestoffen in het bijzonder nuttig is wanneer de fruitvliegenpopulatie klein is, voornamelijk doordat aggregatie door de volwassen vliegen de lokale sterfte van de larven door het Allee effect verminderde (**Hoofdstukken 2 & 4**). In *D. melanogaster* zijn er verschillende mechanismen bekend die bijdragen aan het Allee effect. Ten eerste heeft aggregatie door de volwassen fruitvliegen een positief effect op de overleving van hun larven doordat zij (in het bijzonder de vrouwtjes) gist met zich meedragen, en daardoor de plek waar ze eten, paren en eitjes leggen met gist enten. Dit heeft een positief effect op de overleving van de fruitlarven, want zij leven van gist. Ten tweede remt de toename van gist de groei van schimmels. Dit heeft een positief effect op de larven omdat schimmels een hoge sterfte in fruitvlieglarven kunnen veroorzaken. Ten derde zijn de larven van *D. melanogaster* zelf in staat om de schimmelgroei te remmen door middel van het verstoren van de groei van de hyfen van de schimmel. Grotere groepen van larven doen dat met meer succes dan kleinere groepen.

Spionerende vijanden hebben een effect op de populatiedynamica van de fruitvlieg

De meeste studies naar het effect van informatiestoffen richten zich op plant-herbivoor-sluipwesp of plant-herbivoor-roofdier interacties. In deze studies gebruiken de natuurlijke vijanden vaak herbivoor-geïnduceerde vluchtige plantenstoffen die vrijkomen als de plant wordt aangevallen door herbivoren. **Hoofdstuk 5** behandelt hoe informatiestoffen de interactie tussen een gastheer en een sluipwesp beïnvloedt in een systeem waarin de sluipwesp spioneert op de intra-specifieke communicatie van zijn gastheer (dit is de communicatie die voor individuën binnen een soort bestemd is). Hiertoe is het model uit Hoofdstuk 2 uitgebreid met de populatie van de sluipwesp en de interactie tussen de sluipwesp en de gastheer. Het uitbuiten van de informatiestoffen door de sluipwesp had een negatief effect op de grootte en de groei van de fruitvliegpopulatie. Verder was het gemiddelde parasiteringsniveau hoger wanneer sluipwespen informatiestoffen konden exploiteren. Dit resulteerde in een langzamere groei van de fruitvliegpopulatie. Daardoor duurde het ook langer om de negatieve effecten behorend bij een kleine populatiegrootte – het Allee effect – te overwinnen. Verder was dit negatieve effect sterker aanwezig als fruitvliegen niet in staat waren om informatiestoffen te gebruiken en dus de plekken voor reproductie op een willekeurige wijze moesten vinden.

Een verminderd risico voor predatie of parasitering wordt beschouwd als één van de mogelijke voordelen van het vormen van aggregaties. De simulaties gaven echter geen bewijs voor een lokaal verminderd risico op parasitering bij hogere larvendichtheden. Integendeel, de simulaties gaven juist aan dat proportioneel gezien de sterfte van de larven toenam met hogere dichtheid van larven op een appel.

De simulaties lieten geen verschil zien in de omvang van de fruitvliegpopulatie en in de sterfte van de larven door parasitisme, tussen de situatie waarin de sluipwespen het aggregatieferomoon van de fruitvliegen exploiteerden en de situatie waarin ze alleen maar de geuren van gistende appels konden gebruiken om de larven van de fruitvlieg te vinden. Deze resultaten geven aan dat er voor *D. melanogaster* het gebruik van aggregatieferomoon geen kosten met zich meebrengt in de vorm van een groter risico van parasitisme. Bovendien versterkt het gebruik van informatiestoffen door de gastheer zijn eigen populatiegroei, en het stelt de gastheerpopulatie in staat om bij hogere sluipwespdichtheden te overleven. De simulaties in dit proefschrift laten zien dat op korte termijn de sluipwespen appels met *Drosophila*-larven beter kunnen vinden als zij het aggregatieferomoon van de fruitvlieg kunnen gebruiken; dit komt overeen met de resultaten van experimenten. Op de lange termijn resulteert deze sterkere aantrekking echter niet in meer parasitisme dan wanneer de sluipwespen alleen met de geur van gist de rottende appels konden lokaliseren. De tijd dat *L. heterotoma* op een plek blijft stijgt met het aantal gastheren op die plek. Als de fruitvliegpopulatie groot is, dan zijn er ook meer larven op de appels, en daarom spendeert *L. heterotoma* meer tijd aan het zoeken naar gastheren op een appel en veel minder tijd aan het zoeken van een nieuwe appel met nieuwe gastheren.

Onderscheiden van geuren en het vinden van de meest geschikte locatie

Er is gedetailleerd onderzocht hoe geuren zich in geurpluimen door de lucht verplaatsen, en hoe motten zich in die pluimen oriënteren. In deze onderzoeken was er echter altijd maar één geurbron. In de omgeving van de fruitvlieg zijn meerdere plekken beschikbaar voor reproductie die ook nog kunnen verschillen in geschiktheid voor reproductie. Die geschiktheid kan een fruitvlieg waarnemen door de geuren die van die plek vrijkomen. Een plek die zowel geuren van vergisting (‘voedselgeur’) als aggregatieferomoon afgeeft is geschikter dan een plek met alleen voedselgeur. De concentratie van het aggregatieferomoon speelt ook nog een rol: hoe hoger de concentratie, hoe geschikter de plek is. Omdat het aggregatieferomoon vrijkomt bij het leggen van eitjes is het een goede indicator voor de toekomstige dichtheid van fruitvlieglarven. In **Hoofdstuk 6** ga ik na welke gedragsregels het beste de verplaatsing van een fruitvlieg richting een geurbron kunnen beschrijven, en bij welk gedrag de fruitvlieg succesvol onderscheid kan maken tussen geurbronnen met een verschillende geschiktheid. In dit hoofdstuk gebruik ik een wiskundige methode die fundamenteel verschillend is van de methode gebruikt in Hoofdstuk 2-5. In **Hoofdstuk 2-5**, zijn partiële differentiaalvergelijkingen en integro-differentiaalvergelijkingen voor de verwachte lokale fruitvlieg- en sluipwespdichtheden numeriek opgelost. In **Hoofdstuk 6** daarentegen is een stochastisch model gebruikt om het gedrag van honderden individuele fruitvliegen direct te berekenen. Door de random effecten (in dit stochastische model) moesten deze simulaties meerdere keren herhaald worden om het gemiddelde patroon te kunnen achterhalen.

Gedragsregels voor motten waren ook goed te gebruiken om te beschrijven hoe fruitvliegen de bron van een filamentenpluim te zoeken; een filamentenpluim is een geurpluim die bestaat uit kleine bolletjes (‘filamenten’) geurstof, afgewisseld door stukjes waar geen geur voorkomt. Deze regels waren echter niet afdoende om de fruitvlieg naar de meest geschikte geurbron te leiden; daarvoor is ook nog een voorkeur nodig voor de combinatie van aggregatieferomoon en voedselgeur (“F+A”) boven voedselgeur alleen (“F”). Deze sterkere voorkeur hoeft echter niet aangeboren te zijn. Zolang fruitvliegen in staat zijn om hun huidige voorkeur voor “F+A” te onthouden en aan te passen op basis van waargenomen geurconcentraties, vinden meer fruitvliegen de meest aantrekkelijke geurbron. Dit is ook wat je zou verwachten, omdat bronnen die alleen voedselgeur uitstoten wel potentieel geschikt zijn voor reproductie. In een omgeving waar nog geen aggregatieferomonen aanwezig zijn, hebben alle vliegen die aangetrokken worden door voedselgeur kans om andere individuen tegen te komen. Pas vanaf het moment dat aggregatieferomoon vrij begint te komen – een indicatie dat andere vliegen er eieren hebben gelegd – worden deze “F+A” bronnen de meer geschikte geurbron.

Verder laat deze studie zien dat het aantal vliegen dat een “F+A” bron vond sterk toenam na het toevoegen van de gedragsregel dat fruitvliegen met de wind mee vliegen wanneer ze de pluim met zigzag-bewegingen niet snel genoeg terug vinden. We hebben de resultaten van de simulaties vergeleken met resultaten van een experiment van Wertheim et al. (2002a). Dit liet zien dat de modellen die nu ontwikkeld zijn potentiëel geschikt zijn om het aantal vliegen dat een “F” of een “F+A” bron vindt te schatten. Ze waren echter nog niet in staat om de ruimtelijke verdeling van de fruitvliegen over de verschillende geurbronnen correct te voorspellen.

Algemene conclusie

Dit proefschrift laat zien dat het gebruik van informatiestoffen door *D. melanogaster* effect had op diens populatiedynamica. Het gebruik van informatiestoffen had een positief effect op de goei van kleine populaties en het verbeterde het de kolonisatievermogen van de fruitvlieg. Maar wanneer de populatie groter werd, werden de negatieve effecten van concurrentie tussen de larven groter dan het positieve effect van verminderde sterfte door het Allee effect. Het gebruik van informatiestoffen is echter cruciaal bij het koloniseren van een gebied van buitenaf. De simulaties lieten zien dat populaties van fruitvliegen die geen geuren konden gebruiken niet in staat waren om het gebied te koloniseren en zij stierven uit. Wanneer de natuurlijke vijand, een sluipwesp, informatiestoffen kon gebruiken was de sterfte door parasitisme hoger dan wanneer sluipwespen geen geuren konden gebruiken. Dit resulteerde in een langzamere groei van de fruitvliegpopulatie. Het gebruik van informatiestoffen beïnvloedt ook de interactie tussen de fruitvlieg en de sluipwesp. Het gebruik van informatiestoffen door de fruitvlieg stelde de fruitvliegen in staat om met hogere dichtheden van hun natuurlijke vijand samen te leven.

Wageningen, 1 februari 2012, 01:01 uur

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Curriculum Vitae

Marjolein Elisabeth Lof was born on May 21st 1978 in Groningen, The Netherlands. After finishing secondary school, she started her study Biology at Wageningen University in 1996 and obtained her MSc degree in 2001. During her first master thesis she investigated what factors caused the population decline in Hen Herriers in the Netherlands. In this study she analyzed ringing data of Hen Herriers (*Circus cyaneus*) to gather information on age dependent survival and migration patterns and developed an age structured population model. This study was supervised by Frank van den Bosch. During her second master thesis she investigated the influence of different sized herbivores on the expansion of Blackthorn (*Prunus spinosa*) and the establishment of Oak (*Quercus robur*) in extensively grazed river dunes. In this project she combined field work with spatial modelling, under the supervision of Han Olff and Liesbeth Bakker. After that, she did a short internship at the Centre of Biometrics in Wageningen, where she developed a metapopulation model that included Allee effect and competition.

In 2002, she worked on a short project at the "Rijksinstituut voor Integraal Zoetwaterbeheer en Afvalwaterbehandeling" (RIZA) in Lelystad. In this project, she used GIS to study the effect Climate and Management Scenario's on National fresh water habitats. From 2002 to 2004, she did a two year traineeship ("Rijkstraineeprogramma") at Rijkswaterstaat. During this traineeship, the first half year she worked at "Directie Zeeland" in Middelburg, here she studied the effect of the decline of salt marshes, mudflats and sandbanks, due to the partial closure of the Eastern Scheldt, on population numbers of waders. The second half year she worked at "Rijksinstituut voor Kust en Zee" in Middelburg, here she worked on the (food) ecology of waders in the Eastern Scheldt. The third half year she worked at the Expertise centre of the Ministry of Agriculture, Nature and Food Quality in Ede. Here, she worked in a project on fine-tuning the objectives of the EU Bird Directive, the EU Habitat Directive and the EU Water Framework Directive in nature conservation areas. The last half year of the traineeship, she worked at RIZA in Arnhem, here she continued working on the EU Water Framework Directive.

From June 2004 to November 2008 she did her PhD research at the Department of Mathematical and Statistical methods, under supervision of Lia Hemerik, Maarten de Gee and Marcel Dicke. The research focused on how chemical information affects population dynamics of species in a food chain (this thesis). From January 2009 to April 2009, she did a short modelling study on "how odours guide moths to patches of different sizes" in close collaboration with Peter Hambäck and Petter Anderson of the Department of Botany, Stockholm University. From May 2009 on, she works on "Optimal timing of reproduction of the Great tit (*Parus major*) in a warming world" at the Animal Ecology Department of Marcel Visser, at the Netherlands Institute of Ecology (NIOO) in Wageningen.

Publications

M.E. Lof, R. Etienne, J. Powell, M. de Gee, L. Hemerik, 2008. The effect of chemical information on the spatial distribution of fruit flies I Model results. Bull. Math. Biol. 70, 1827-1849.

M. de Gee, **M.E. Lof**, L. Hemerik, 2008. The effect of chemical information on the spatial distribution of fruit flies II Parameterization, calibration and sensitivity. Bull. Math. Biol. 70, 1850-1868.

M.E. Lof, M. de Gee, L. Hemerik, 2010. Odour mediated aggregation enhances the colonization ability of Drosophila melanogaster. J. Theor. Biol. 258, 363-370.

M.E. Visser, L te Marvelde, **M.E. Lof**, 2012. Adaptive mismatches of birds and their food in a warming world. J. Ornithol. DOI 10.1007/s10336-011-0770-6.

Submitted

M.E. Lof, M. de Gee, M. Dicke, L. Hemerik. A spatio-temporal model with odour-mediated parasitoid-host interactions. Submitted.

M.E. Lof, T. Reed, J.M. McNamara, M.E. Visser. Timing in a fluctuating environment: environmental variability and asymmetric fitness curves can lead to adaptively mismatched avian reproduction. Submitted.

Other publications

Scientific

Etienne, R.S., **M.E. Lof**, L. Hemerik, 2002. The Allee effect in metapopulation dynamics revisited. In: Etienne R.S. Striking the metapopulation balance. Mathematical models and methods meet metapopulation management. pp. 71-78. PhD Thesis, Wageningen University, Wagenininingen, The Netherlands.

M.E. Lof, L. Hemerik, M. de Gee, 2007. Chemical communication: does odor plume shape matter? Proc. Neth. Entomol. Soc. Meet. 18, 61-70.

Policy

M.E. Lof, D. van der Molen, 2002. Effecten van klimaatverandering op de ecotopen en de natuur van de rijkswateren in 2050. RIZA werkdocument 2002.175X, RIZA, Dictoraat-Generaal Rijkswaterstaat, Ministerie van Verkeer en Waterstaat.

M.E. Lof, 2003. Zandhonger, slokt de Oosterschelde het voedsel van de vogels op? Werkdocument DZL/AXA 03.19, Directie Zeeland, Dictoraat-Generaal Rijkswaterstaat, Ministerie van Verkeer en Waterstaat.

V. van den Berk, T. Brandwijk, C. van Dam, M. Fellinger, A. Hagendoorn, A. Lassche, **M. Lof**, V. van der Meij, J. Olink, W. Schaap, 2004. Vis à vis: Evaluatie beleidsbesluit binnenvisserij. Rapport EC-LNV nr 2004/296. Expertisecentrum LNV, Ministerie van Landbouw, Natuur en Visserij.

M. Felinger, T. Kok, **M. Lof**, V. van der Meij, 2004. Stroomlijning Kaderrichtlijn Water en Habitatrichtlijn. Rapport EC-LNV nr 2004/349. Expertisecentrum LNV, Ministerie van Landbouw, Natuur en Visserij.

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- Spatio-temporal modelling of infochemicals in a food web context (2004)

Post-graduate courses (8.4 ECTS)

- The art of modelling; PE&RC & SENSE (2004)
- Spatio-temporal models in ecology: an introduction to integro difference equations; PE&RC, self study (2004)
- Spring School chemical communications; PE&RC (2005)
- Spatial and temporal aspects in resource ecology; PE&RC (2005)

Laboratory training and working visits (7.5 ECTS)

- Integro-difference modelling; Dept. of Mathematics and Statistics, Utah State University (2005)

Invited review of (unpublished) journal (1 ECTS)

- Theoretical Population Biology: sudden dynamical change in spatial population models (2009)

Deficiency, refresh, brush-up courses (12 ECTS)

- Applied partial differential equations; Mathematical and Statistical Methods (2005)
- Capita selecta complex population dynamics; Crop and Weed Ecology (2006)

Competence strengthening / skills courses (4.8 ECTS)

- Workshop scientific publishing; WGS (2004)
- PhD Competence assessment; WGS (2006)
- Scientific writing; WGS (2007)
- Writing a grant proposal; WGS (2007)
- Programming in R; Biometris (2007)

PE&RC Annual meetings, seminars and the PE&RC weekend (3 ECTS)

- PE&RC Day “Biological Catastrophes”(2004)
- Introduction weekend (2005)
- PE&RC Day “Truth of Science” (2005)
- Introduction weekend (2006)
- PE&RC Day “The Scientific Agenda” (2006)
- PE&RC Day “Collapse” (2007)

Discussion groups / local seminars / other scientific meetings (6.9 ECTS)

- Statistics, Maths and Modelling in PE&RC (2004-2008)
- PhD Lunch Entomology (2005-2006)
- NVTB-days (2-day annual meeting of Dutch Society for Theoretical Biology; oral presentation; Schoorl, the Netherlands (2005-2007)
- NEV-days (1-day annual meeting of the Dutch Entomological Society; oral presentation; Ede, the Netherlands (2006-2007)

International symposia, workshops and conferences (8.2 ECTS)

- 12th Benelux Congress of Zoology; Wageningen, the Netherlands (2005)
- 14th Benelux Congress of Zoology; Amsterdam, the Netherlands (2007)
- 3rd International Symposium on Computational Life Science; Utrecht, the Netherlands (2007)
- 2nd Congress on Computational and Mathematical Population Dynamics; Campinas, Brazil (2007)

Lecturing / supervision of practical’s / tutorials; 40 day

- Wiskunde T – Linear Algebra; lecture (2005-2007)
- Models of Biological Processes and Environmental Quality; practical supervision (2006)

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