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Marjolein E. Lof, Maarten de Gee, Lia Hemerik. Odor mediated aggregation enhances the colonization ability of. *Journal of Theoretical Biology*, 2009, 258 (3), pp.363. 10.1016/j.jtbi.2008.08.019 . hal-00554505

HAL Id: hal-00554505

<https://hal.science/hal-00554505>

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Author's Accepted Manuscript

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PII: S0022-5193(08)00420-7
DOI: doi:10.1016/j.jtbi.2008.08.019
Reference: YJTBI 5254

To appear in: *Journal of Theoretical Biology*

Received date: 1 February 2008
Revised date: 9 June 2008
Accepted date: 7 August 2008

Cite this article as: Marjolein E. Lof, Maarten de Gee and Lia Hemerik, Odor mediated aggregation enhances the colonization ability of *Drosophila melanogaster*, *Journal of Theoretical Biology* (2008), doi:[10.1016/j.jtbi.2008.08.019](https://doi.org/10.1016/j.jtbi.2008.08.019)

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Odor 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 successfully 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. Odor 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 pheromone · Spatial population dynamics · Allee effect · Competition

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 (Rohlf et al., 2005, Rohlf, 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 (Rohlf et al., 2005, Rohlf, 2008). The local interaction with the fungi gives rise to an Allee effect in larval development. However, aggregation formation can also have negative effects. Rohlf 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 Rohlf, 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, Rohlf, 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 *Drosophila 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., in press). 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 center 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 odor distribution and population responses (as in Lof et al., in press). 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.

2. Description of the model

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 P_S) uses chemical information to find a suitable resource, a yeast infected apple. Once they found a resource, they settle down with a rate λ (min^{-1}). They become part of settled subpopulation (with density P_R), whose members forage and mate on the resource. Members of the settled subpopulation have a leaving rate from the resource of α_1 (min^{-1}). In doing so they join the moving subpopulation (with density P_M), which actively move away from the resource. A member of the moving population starts to search for a new resource with rate α_2 (min^{-1}) and becomes a member the searching subpopulation. The equations relating these state variables are

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

$$\frac{\partial}{\partial t} P_S = \alpha_2 P_M - \lambda R P_S \quad (2)$$

$$\frac{\partial}{\partial t} P_R = \lambda R P_S - \alpha_1 P_R \quad (3)$$

$$\frac{\partial}{\partial t} P_M = \alpha_1 P_R - \alpha_2 P_M \quad (4)$$

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 (P_S) 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 χ . When chemical information is absent, the searching population can only disperse randomly, with dispersal coefficient D_P . The fruit fly response to food odors (with density F) and the aggregation pheromone (with density A) is modeled as a Monod function (Monod, 1949). Bartelt et al (1985) showed that fruit flies respond to the combination of food odors and the aggregation pheromone and are also attracted to food odors alone. They however, do not respond to the aggregation pheromone without food odors also present. Equation 6 gives a description of the response of *D. melanogaster* to food odors and the aggregation pheromone

$$\frac{\partial}{\partial t} P_S = D_P \nabla^2 P_S - \nabla \cdot [\chi P_S \nabla f(F, A)] \quad (5)$$

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

where F_0 and A_0 are the concentrations of food odors 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 odors and the aggregation pheromone as compared to the response to only food odors.

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 odors 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 modeled with ordinary or partial differential equations; in an integro-difference equation it is

modeled with a ring random dispersal kernel (Lof et al., in press). 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.

$$L(x, y, n) = \int_0^3 \xi P_R(x, y, n) dt . \quad (7)$$

$$P_S(x, y, n+1) = \phi L(x, y, n) s_A(L) s_C(L) , \quad (8)$$

$$s_A(L) = \frac{1}{1 + e^{-c_A(L-L_A)}} , \quad s_C(L) = \frac{1}{1 + e^{c_C(L-L_C)}}$$

The descriptions and values of all parameters in our model are given in Table 1.

2.2 Odor distribution

D. melanogaster responds to food odors (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 odors thus diffuse randomly, i.e. going in any direction with an equal probability. Turbulent odor diffusion is a much faster process than the dispersal of adult fruit flies. Because odor diffusion is a 3-dimensional process, while we model in two dimensions, we introduced a loss term (μ) to represent odor molecules that gets out of reach of the searching population through diffusion in a vertical direction.

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

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

$$\frac{\partial}{\partial t} A_R = \theta_A P_R - \omega A_R \quad (11)$$

The description and value of the parameters are given in Table 1. For more details on how these values are arrived at, we refer to de Gee et al. (in press).

2.3 Numerical approach

In the numerical solution of the model equations, the odor and fruit fly dispersal was treated separately from the adult fruit fly population dynamics. Odor distribution, odor 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.

Odor distribution and odor evaporation

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

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

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

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

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

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

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

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

Dispersion of the searching population

The movement of the searching population (P_S) is directed towards the odor 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)

$$\frac{\partial}{\partial t} \tilde{P}_S = D_P \nabla^2 \tilde{P}_S + v \nabla f(F, A) \cdot \nabla \tilde{P}_S \quad (15)$$

where,

$$P_S = \tilde{P}_S \cdot \exp\left(-\frac{v}{D_P} f(F, A)\right) \quad (16)$$

with,

$$\tilde{P}_S(x, y, 0) = \exp\left[-\frac{v}{D_P} f(F, A)\right] P_S(x, y, 0) \quad (17)$$

and advancing P_S using a truncated asymptotic series approximation for $\tilde{P}_S$,

$$\tilde{P}_S(t) \approx \sum_0^i v^i \tilde{P}_i(x, y, t) \quad (18)$$

with,

$$\tilde{P}_0(x, y, T) = K(x, y, T) * \tilde{P}_0(x, y, 0)$$

$$\tilde{P}_i(x, y, T) = \int_0^T K(x, y, T-t) * [\nabla f \cdot \nabla \tilde{P}_{i-1}(t)], \quad \text{for } i \geq 1, \tilde{P}_i(x, y, 0) = 0$$

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

3. Simulation set-up

We considered a spatial domain of 90 m × 90 m, with the orchard in the center. 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 eliminated the unwanted effects of these boundary conditions, the 90 m × 90 m domain was embedded in the center 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 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.

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 $\kappa = v/D_P$ 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 behavior at four levels of κ namely: no attraction, that is, random dispersal only ($\kappa=0$), weak attraction ($\kappa=1$), intermediate attraction ($\kappa=5$) and strong attraction ($\kappa=10$).

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 center of the domain (60 m $\times$ 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. 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 three 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 ($\kappa=1$, $\kappa=5$ and $\kappa=10$). 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 $\times$ 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. 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). 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 ($\kappa=0$) was significantly lower ($G=10.650$, $G=16.527$ and $G=22.422$, $P < 0.001$ for $\kappa=1$, 5 and 10 respectively), around 15-20 % (Fig. 5). This indicates that the use of chemical information induces aggregation on the resources.

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 ($\kappa=0$): 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 $\kappa=1$, 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 $\kappa=5$ and $\kappa=10$ ($G=14.335$, $G=47.464$, both $P < 0.001$) were significantly lower than for $\kappa=1$, and the mortality for $\kappa=10$ was also significantly lower than for $\kappa=5$ ($G=10.708$, $P < 0.0025$). 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 $\kappa=5$ and $\kappa=10$ was stronger than for $\kappa=0$ and $\kappa=1$ $P < 0.001$, and the latter was stronger than for $\kappa=0$, $P < 0.001$). 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.

Summarizing, 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.

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. Rohlf 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.

Acknowledgements

M.E.L. was subsidized by the Computational Life Sciences program of the Netherlands Organization for Scientific Research (NWO, project number 635.100.011). The authors would like to thank Gerrit Gort for his help with the linear mixed effect models, and Marcel Dicke and three anonymous referees for their valuable comments on an earlier draft of the manuscript.

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Table 1 The model parameters involved in the short time dynamics and their values.
For dimensionless parameters the ‘-’ sign is used.

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

Figure legends

Fig. 1 Spatial set-up of the domain (90 m $\times$ 90 m). The resources are randomly distributed in the center of the domain (60 m $\times$ 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.

Fig. 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).

Fig. 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).

Fig. 4 Larval mortality due to the Allee effect (solid lines) and competition (dotted 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 ($\kappa = 0$, red square) and for the simulations with weak (circle), intermediate (triangle) and strong (diamond) attraction to infochemicals ($\kappa = 1, 5$ and 10, respectively). Note that in 4a) the larval mortality for $\kappa = 0$ is given for the first three generations only, because the population got extinct after the third generation

Fig. 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 ($\kappa = 0$, 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). Note that the percentage of settlement for $\kappa = 0$ is given for the first three generations only, because the population got extinct after the third generation.

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