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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

50 effects, known as the Allee effect (Allee, 1931), or a reduced per capita growth rate at
51 low population densities, can for instance occur due to difficulties in finding a mate or
52 difficulties in resource exploitation (Wertheim et al., 2005). Protection from predators
53 is viewed as an important selective advantage to group membership resulting from
54 aggregation (Parrish and Edelman-Keshet, 1999, Wertheim et al., 2005). Protection
55 from environmental conditions can also be a benefit from aggregation (see for
56 instance Gilbert et al., 2006). Furthermore, in temporary habitats (e.g. habitats in early
57 stages of ecological succession, ephemeral ponds, annual plants or fermenting fruits)
58 aggregation is generally considered to promote coexistence of species competing for
59 resources, by reducing the impact of interspecific competition relative to that of
60 intraspecific competition (Atkinson and Shorrocks, 1981, Shorrocks and Sevenster,
61 1995, Krijger and Sevenster, 2001). However, aggregation also involves costs,
62 individuals within an aggregation frequently experience more severe competition for
63 food, space and mates than when they would be on their own. Moreover, within a
64 group a pathogen can be more easily transmitted, than between solitary individuals.
65 Also the group as a whole can be more conspicuous to natural enemies (Parrish and
66 Edelman-Keshet, 1999).

67 In *Drosophila melanogaster* adult aggregation has a positive effect on larval
68 survival because adults alter the suitability of the resource for the juveniles: the
69 presence of adults prior to larval development increases the amount of food that is
70 present for the larvae. Adults, especially females, vector a diversity of yeasts and
71 inoculate the resource with these yeasts during their presence (Morais et al., 1995). At
72 the same time, this increase in yeast also reduces fungal growth (Wertheim et al.,
73 2002). This positively affects larval survival, because strong fungal growth can cause
74 a high mortality in fruit fly larvae (Rohlf et al., 2005, Rohlf, 2006). Furthermore the
75 larva of *D. melanogaster* themselves are also able to suppress fungal growth by
76 disrupting the hyphae of the fungus. Larger groups of larva are more successful at this
77 than smaller groups or single larvae (Rohlf et al., 2005, Rohlf, 2008). The local
78 interaction with the fungi gives rise to an Allee effect in larval development.
79 However, aggregation formation can also have negative effects. Rohlf and
80 Hoffmeister (2003) show that the survival from egg to adulthood for *Drosophila*
81 *subobscura* is hump shaped, with low survival not only at low population numbers but
82 also at high population numbers. This indicates the presence of a cost to aggregation.
83 At high local population densities larval survival decreases due to competition
84 (Wertheim et al., 2002, Hoffmeister and Rohlf, 2001).

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

95 The fruit fly *Drosophila melanogaster* breeds in ephemeral substrates, e.g.
96 fermenting fruit. In their natural environment these substrates are distributed
97 unevenly. Fermentation products, produced by micro-organisms that live on food
98 sources, and aggregation pheromone, emitted by recently mated females, play through
99 chemical attraction a directive role in the localization of and aggregation on these

100 substrates (Hutner et al., 1937; West, 1961; Bartelt et al., 1985; Wertheim et al.,
101 2006).

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

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

130
131

132 **2. Description of the model**

133
134

135 **2.1 Population dynamics and dispersal of fruit flies**

136
137

Within-generation dynamics

138 In our model, we consider female fruit flies only. This female fruit fly population is
139 divided according to three activities they can exhibit. The searching subpopulation
140 (with density P_S) uses chemical information to find a suitable resource, a yeast
141 infected apple. Once they found a resource, they settle down with a rate λ (min^{-1}).
142 They become part of settled subpopulation (with density P_R), whose members forage
143 and mate on the resource. Members of the settled subpopulation have a leaving rate
144 from the resource of α_1 (min^{-1}). In doing so they join the moving subpopulation (with
145 density P_M), which actively move away from the resource. A member of the moving
146 population starts to search for a new resource with rate α_2 (min^{-1}) and becomes a
147 member the searching subpopulation. The equations relating these state variables are
148

$$149 \quad R(x, y) = \begin{cases} 0 & \text{if no apples are present at position } (x, y) \text{ at time } t \\ 1 & \text{if an apple is present at position } (x, y) \text{ at time } t \end{cases} \quad (1)$$

$$150 \quad \frac{\partial}{\partial t} P_S = \alpha_2 P_M - \lambda R P_S \quad (2)$$

$$151 \quad \frac{\partial}{\partial t} P_R = \lambda R P_S - \alpha_1 P_R \quad (3)$$

$$152 \quad \frac{\partial}{\partial t} P_M = \alpha_1 P_R - \alpha_2 P_M \quad (4)$$

153

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

162

163 *Fruit fly dispersal*

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

176

$$177 \quad \frac{\partial}{\partial t} P_S = D_p \nabla^2 P_S - \nabla \cdot [\nu P_S \nabla f(F, A)] \quad (5)$$

$$178 \quad f(F, A) = \frac{F}{F_0 + F} + \eta \frac{FA}{F_0 A_0 + FA} \quad (6)$$

179

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

184 While the movement of searching fruit flies is directed by chemical
 185 information, the movement away from the resource by the moving fruit fly population
 186 is not affected by the presence of food odors and the aggregation pheromone. The
 187 fruit flies come into the moving state by actively flying away from their resources. We
 188 assume that the fruit flies actively fly away with a velocity ρ from the resource in an
 189 arbitrary direction and afterwards disperse randomly. This process cannot be modeled
 190 with ordinary or partial differential equations; in an integro-difference equation it is

191 modeled with a ring random dispersal kernel (Lof et al., in press). We chose this type
 192 of dispersal to ensure that the majority of the moving population actually leaves the
 193 resource. If the population were to start searching for a resource immediately by using
 194 chemical information, the majority of the fruit flies would return to the same resource.

195 *Between-generation dynamics: reproduction*

196 Per generation, lasting 21 days in reality, we simulated three dispersal days, during
 197 which fruit flies are actively dispersing and reproducing. Adult females that have
 198 settled on a resource deposit ξ eggs per minute on average. The cumulative number of
 199 eggs on a resource after the 3 days (in generation n (Eq. 7)) determines whether larvae
 200 develop successfully into adult fruit flies in the next discrete generation. The larvae
 201 develop into adults in 18 days. We do not model the development explicitly, but we
 202 only calculate what fraction of the larvae survive and constitute the next generation.
 203 The fraction of the larvae that survive on one resource are highest for intermediate
 204 numbers of larvae (Eq. 8). When only a small number of larvae is present on an apple,
 205 a fraction dies due to the Allee effect, while mortality due to competition plays a role
 206 when many larvae are present. Of the surviving larvae, a fraction ϕ is female. At the
 207 end of a generation the total adult population dies and half of the surviving larvae
 208 constitute the next adult female generation. Furthermore, we assume that at the end of
 209 a generation all resources are either depleted or unsuitable for reproduction.
 210 Therefore, there is no resource anymore at the beginning of the next generation when
 211 the new adults emerge from the pupae. The new generation of adult fruit flies has to
 212 start searching for a new resource immediately. In our simulation these resources are
 213 randomly placed at the beginning of each generation.
 214

$$215 \quad L(x, y, n) = \int_0^3 \xi P_R(x, y, n) dt . \quad (7)$$

$$216 \quad P_S(x, y, n+1) = \phi L(x, y, n) s_A(L) s_C(L) ,$$

$$217 \quad s_A(L) = \frac{1}{1 + e^{-c_A(L-L_A)}} , \quad s_C(L) = \frac{1}{1 + e^{c_C(L-L_C)}} \quad (8)$$

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

219 2.2 Odor distribution

220 *D. melanogaster* responds to food odors (F) and its aggregation pheromone (A).
 221 Aggregation pheromone is not excreted as a volatile, but as a fluid accompanying the
 222 eggs. We therefore divide the aggregation pheromone in two phases: a liquid or
 223 adsorbed form (with density A_R) at the resource, that slowly evaporates into a gaseous
 224 form (A) that searching fruit flies can detect in the air. We assume that no wind is
 225 present and that these odors thus diffuse randomly, i.e. going in any direction with an
 226 equal probability. Turbulent odor diffusion is a much faster process than the dispersal
 227 of adult fruit flies. Because odor diffusion is a 3-dimensional process, while we model
 228 in two dimensions, we introduced a loss term (μ) to represent odor molecules that gets
 229 out of reach of the searching population through diffusion in a vertical direction.
 230
 231
 232
 233

$$234 \quad \frac{\partial}{\partial t} F = D_I \nabla^2 F - \mu F + \theta_F R \quad (9)$$

$$235 \quad \frac{\partial}{\partial t} A = D_I \nabla^2 A - \mu A + \omega A_R \quad (10)$$

$$236 \quad \frac{\partial}{\partial t} A_R = \theta_A P_R - \omega A_R \quad (11)$$

237

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

240

241 2.3 Numerical approach

242

243 In the numerical solution of the model equations, the odor and fruit fly dispersal was
244 treated separately from the adult fruit fly population dynamics. Odor distribution, odor
245 evaporation and dispersal by the moving and searching fruit fly population were
246 solved using the integro-difference approach (as in Neubert et al., 1995, Powell et al,
247 1998). In this approach, dispersion is treated as a process separately occurring in time.
248 The analytical solution of this process is used in the simulation model. This is an
249 effective approach, because it allows us to take large time steps, without running into
250 any numerical stability problems.

251

252 *Odor distribution and odor evaporation*

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

256

$$257 \quad K(x, y, \Delta t) = \frac{1}{4\pi D_I \Delta t} e^{-\frac{x^2 + y^2}{4D_I \Delta t}} \quad (12)$$

258

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

260

261 During each time step, food odors and the aggregation pheromone evaporate
262 into the air. The dispersal of the produced odor is calculated by taking the convolution
263 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

$$264 \quad K(x, y, \Delta t) = \int_0^{\Delta t} \frac{1}{4\pi D_I t} e^{-\frac{x^2 + y^2}{4D_I t}} dt = \frac{1}{4\pi D_I} Ei\left(\frac{x^2 + y^2}{4D_I \Delta t}\right) \quad (13)$$

265

266 where Ei is the exponential integral.

267

268 *Ring random dispersal*

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

271

$$272 \quad K(x, y, \Delta t) = \frac{1}{4\pi D_p \Delta t} e^{-\frac{(\sqrt{x^2 + y^2} - \rho \Delta t)^2}{4D_p \Delta t}} \quad (14)$$

273

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

276

277 *Dispersion of the searching population*

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

$$282 \quad \frac{\partial}{\partial t} \tilde{P}_S = D_P \nabla^2 \tilde{P}_S + v \nabla f(F, A) \cdot \nabla \tilde{P}_S \quad (15)$$

283 where,

$$284 \quad P_S = \tilde{P}_S \cdot \exp\left(-\frac{v}{D_P} f(F, A)\right) \quad (16)$$

285 with,

$$286 \quad \tilde{P}_S(x, y, 0) = \exp\left[-\frac{v}{D_P} f(F, A)\right] P_S(x, y, 0) \quad (17)$$

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

288

$$289 \quad \tilde{P}_S(t) \approx \sum_0^i v^i \tilde{P}_i(x, y, t) \quad (18)$$

290 with,

$$291 \quad \begin{aligned} \tilde{P}_0(x, y, T) &= K(x, y, T) * \tilde{P}_0(x, y, 0) \\ \tilde{P}_i(x, y, T) &= \int_0^T K(x, y, T-t) * [\nabla f \cdot \nabla \tilde{P}_{i-1}(t)], \quad \text{for } i \geq 1, \tilde{P}_i(x, y, 0) = 0 \end{aligned}$$

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

293

294

295 3. Simulation set-up

296

297

298 We considered a spatial domain of 90 m \times 90 m, with the orchard in the center. It is
299 divided into 512 \times 512 cells with a diameter of 0.1758 m*. The simulations were
300 carried out with an IDE method that intrinsically uses periodic boundary conditions.
301 To eliminated the unwanted effects of these boundary conditions, the 90 m \times 90 m
302 domain was embedded in the center of an enlarged domain of 180 m \times 180 m. On this
303 large domain, the actual simulations were done. This setup is the best approximation
304 of a real world situation, where the domain containing the orchard is neither
305 surrounded by a wall of doom, nor by a reflecting wall, nor by periodic boundary
306 conditions; instead, there is an unspecified surrounding, into which the flies may enter
307 and from which they may return, driven by random dispersion and chemotaxis. Of
308 course, this surrounding area has an outer boundary again, but this is so far from the
309 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.

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

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

323 We ran the simulation for a resource density of $0.1 \text{ apples m}^{-2}$, representing an
324 orchard where resources are scarce. The resources were randomly distributed in the
325 center of the domain ($60 \text{ m} \times 60 \text{ m}$). To mimic the natural situation, for each
326 generation of flies, the apples were randomly placed. In the initial set-up, we
327 established a 5 meter-wide buffer zone without apples or adult fruit flies around the
328 area containing apples. At the beginning of the simulation we released 1000 adult fruit
329 flies, randomly distributed in a 5 meter-wide zone around the buffer zone outside the
330 orchard (Fig. 1). We ran the simulation three times to verify the consistency of the
331 results.

332 333 *Statistics*

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

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

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

360

361

362 **4. Results**

363

364

365 The presence of chemical information had a positive effect on the ability of fruit flies
366 to colonize an orchard (Fig. 2). The stronger they responded to chemical information,
367 the faster the population was able to find the orchard (Fig. 2). The total population in
368 the orchard for each time step was significantly higher for increasing attraction to
369 infochemicals ($P < 0.0001$ for all combinations of treatments). Furthermore, the
370 population growth was faster for stronger attraction to infochemicals (Fig. 3a). When
371 fruit flies could not respond to chemical information, and thus only dispersed
372 randomly, the population was not able to colonize the orchard. The population went
373 extinct within 4 generations, – population numbers of less than 1 fruit fly in all three
374 runs (combined Fig 2 and 3a). This was mainly caused by a high larval mortality due
375 to the Allee effect: around 90% per generation until the population became extinct
376 (Fig. 4a).

377

378 The number of fruit flies that found the orchard, as well as, the number of fruit
379 flies within the orchard that found a resource and settled down, differed between the
380 situations where fruit flies had the ability to use chemical information or not; the
381 settlement when fruit flies could respond to chemical information was around 40-
382 45%, while the settlement when they could not respond to chemical information ($\kappa=0$)
383 was significantly lower ($G=10.650$, $G=16.527$ and $G=22.422$, $P \ll 0.001$ for $\kappa=1$, 5
384 and 10 respectively), around 15-20 % (Fig. 5). This indicates that the use of chemical
385 information induces aggregation on the resources.

386

387 When fruit flies could respond to chemical information, the mortality due to
388 the Allee effect in the first generation was significantly lower than when they
389 dispersed randomly ($\kappa=0$): between 50 and 70 % for a weak respectively strong
390 attraction towards infochemicals (Fig. 4) ($G=22.261$, $G=47.448$ and $G=73.731$,
391 $P \ll 0.001$ for $\kappa=1$, 5 and 10 respectively). The mortality due to the Allee effect in the
392 first generation was significantly lower for stronger attraction to infochemicals; the
393 mortality for $\kappa=5$ and $\kappa=10$ ($G=14.335$, $G=47.464$, both $P \ll 0.001$) were significantly
394 lower than for $\kappa=1$, and the mortality for $\kappa=10$ was also significantly lower than for
395 $\kappa=5$ ($G=10.708$, $P < 0.0025$). Moreover, there was a significant trend in time, i.e. the
396 mortality due to the Allee effect decreased significantly and mortality due to
397 competition increased significantly (both $P \ll 0.001$). The mortality due to the Allee
398 effect decreased more rapidly for stronger attraction to chemical information (the
399 decrease for $\kappa=5$ and $\kappa=10$ was stronger than for $\kappa=0$ and $\kappa=1$ $P \ll 0.001$, and the
400 latter was stronger than for $\kappa=0$, $P \ll 0.001$). The reduction in the mortality due to the
401 Allee effect is caused by aggregation on the available resources in response to
402 infochemicals. However, this aggregation also caused an increase in mortality due to
403 competition. Still, the presence of chemical information had a net positive effect on
404 population numbers (Fig. 3a).

405

406 In our simulations where we assume that the Allee effect does not have an
407 effect on larval survival, we also found that the ability respond to chemical
408 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,

409 because the population reached its carrying capacity set by competition. If however,
410 the Allee effect played a role, the fruit fly population just reached its carrying capacity
411 in the tenth generation, and only for the fruit fly populations that were strongly
412 attracted to chemical information (Fig 3a). As expected, even when the Allee effect is
413 absent, fruit flies unable to use chemical information still have more difficulties in
414 colonizing the orchard. After the first generation they decrease in number. From the
415 second generation on there is a very slow population growth (from 190 to 245 fruit
416 flies), and they are able to persist 10 generations. It should be noted that after 10
417 generations the total number of fruit flies is only one fourth of the initial population
418 size. If we would simulate multiple breeding seasons, the population would not be
419 able to persist. To check whether this slow growth was due to the fact that we started
420 with a too small number of fruit flies, or just due to the fact that they could only
421 disperse randomly, we simulated random dispersal with an initial population of 2000
422 and 2500 fruit flies. These simulations showed the same results of initial decrease
423 after the first generation and then slow growth. This indicates that the slow growth
424 was mainly because they had more difficulties in finding a resource. As in the
425 simulations including an Allee effect, the settlement of the random dispersing
426 population was only around 15-20 % each generation. Due to this lower settlement,
427 fewer eggs are laid and thus the population growth is less strong. What also plays a
428 role for the reproduction is that a larger part of the fruit flies left the orchard. At the
429 end of a generation only 70% was still in the orchard, while when they were able to
430 respond to chemical information 95-98% remained in the orchard.

431
432 Summerizing, the simulations show that the use of chemical information is crucial for
433 colonizing an area when an Allee effect plays a role, as a random dispersing
434 population was not able to overcome the Allee effect associated with small population
435 sizes. However also without an Allee effect, the random dispersing population had a
436 much lower population growth, and at the end of generation 10 the total number of
437 fruit flies was much lower than the initial population. Indicating that the population is
438 unable to persist multiple breeding seasons, when fruit flies have to colonize the area
439 at the beginning of each breeding season. The use of chemical information is not
440 without costs; at large population sizes aggregation causes competition at the
441 resources and thus increased mortality due to competition.

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444 **5. Conclusions and discussion**

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447 We found that the presence of chemical information is essential for population
448 persistence when resources are scarce. During colonization of an area, populations
449 that cannot use chemical information suffer from extremely high larval mortality
450 (>90%) due to the Allee effect. This was mainly because these populations had more
451 difficulties in locating a resource and were not able to aggregate on suitable resources.
452 Even when the Allee effect did not play a role, the random dispersing population had
453 more difficulties in colonizing the area. Difficulties in locating the resources caused
454 that the population could only grow very slowly. At the end of the breeding season the
455 population size was only one fourth of the initial adult population, indicating that the
456 population is doomed to extinction in the long run. When the fruit flies had the ability
457 to respond to chemical information, the settlement (%) on the resources was much
458 higher, because more fruit flies were able to find the resources, and consequently the

459 mortality due to the Allee effect was much lower. This increased settlement indicates
460 that the response to chemical information causes aggregation on the available
461 resources. However, the use of chemical information is costly - aggregation on the
462 resources also causes an increase in mortality due to competition. Still, there is an
463 overall net positive effect of the use of chemical information on population numbers
464 during population growth. The mortality due to competition can be quite severe
465 especially when the attraction towards chemical information is high: 40 to 60% larval
466 mortality. High mortality due to competition does, however, not have the same
467 dramatic effect on population size as mortality due to the Allee effect. For mortality
468 between 50 and 55%, the population size remains constant. If mortality is higher than
469 55 % the population decreases and if it is lower than 50% the population increases.
470 Nonetheless, if we were to look at individual level the costs of using chemical
471 information could be severe.

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

487 This study partly explains why fruit flies use chemical information in spite of
488 the costs of increased mortality. Chemical information is not only used by fruit flies,
489 but can also be misused by a natural enemy that uses it to find its host (Dicke et al.,
490 1994). The most important natural enemies of *Drosophila* are larval parasitoids
491 (Janssen et al., 1988). Wertheim et al. (2006) found that in the field 67% of apples
492 contained larva of a *Drosophila* species that were parasitized by the larval parasitoids
493 of the genus *Leptopilina*. We plan to investigate the role of chemical information in
494 spatial host-parasitoid interaction. It has been postulated, in the “selfish herd” theory,
495 that individuals in an aggregation experience a diluted risk of attack from natural
496 enemies (Parrish and Edelstein-Keshet, 1999; Wertheim et al., 2005). If this is true,
497 attraction towards chemical information has a positive effect on population numbers
498 by decreasing the risk of parasitism. Rohlf and Hoffmeister (2004) did indeed find
499 that the risk of parasitism could decrease for higher numbers of larva of *Drosophila*
500 *subobscura* in apples and plums. This was mainly because at higher larval densities
501 the larvae could move deeper into the resource, which provides a spatial refuge
502 against larval parasitoids. On the other hand, Wertheim et al. (2003) found that the
503 aggregation pheromone used by *D. melanogaster* to aggregate on a resource also
504 attracted parasitoids towards the resources. Consequently, the percentage of larvae
505 that were parasitized was significantly higher in substrates with aggregation
506 pheromone than in control substrates without aggregation pheromone. This indicates
507 that there is an ecological cost to the use of aggregation pheromone. To get a more
508 complete picture of why *Drosophila* species use chemical information, we will focus

509 on the positive and negative effects of using the *Drosophila* aggregation pheromone
 510 on larval survival and net population numbers of *D. melanogaster* in spatial
 511 parasitoid-host model.

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

520

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522

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528

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612 **Table 1** The model parameters involved in the short time dynamics and their values.
 613 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	-

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616 **Figure legends**

617

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

622

623 **Fig. 2** The dynamics of the total fruit fly population in the orchard (60x60m) in the
 624 first generation, consisting of 3 dispersal days, when fruit flies could not use chemical
 625 information ($\kappa = 0$, solid red line), when the attraction to infochemicals was weak ($\kappa =$
 626 1, dashed line), intermediate ($\kappa = 5$, dash dotted line), or high ($\kappa = 10$, dotted line).

627

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

633

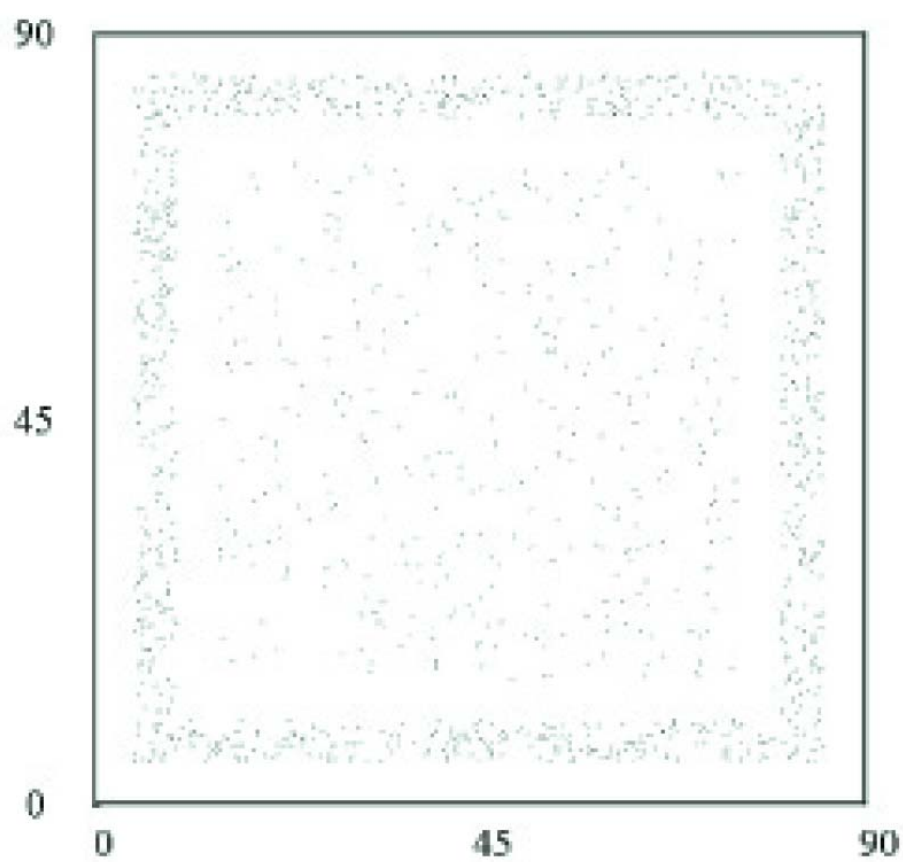
634 **Fig. 4** Larval mortality due to the Allee effect (solid lines) and competition (dotted
 635 lines) for each generation a) with an Allee effect, b) without an Allee effect, for the
 636 control simulation where fruit flies could not respond to chemical information ($\kappa = 0$,
 637 red square)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

641

642 **Fig. 5** The dynamics of the settlement (%) of fruit fly population in the orchard
 643 (60x60m) for all 10 generations for the simulations including an Allee effect, when
 644 fruit flies could not use chemical information ($\kappa = 0$, solid red line), when the
 645 attraction to infochemicals was weak ($\kappa = 1$, dashed line), intermediate ($\kappa = 5$, dash
 646 dotted line), or high ($\kappa = 10$, dotted line). Note that the percentage of settlement for κ
 647 = 0 is given for the first three generations only, because the population got extinct
 648 after the third generation.

649

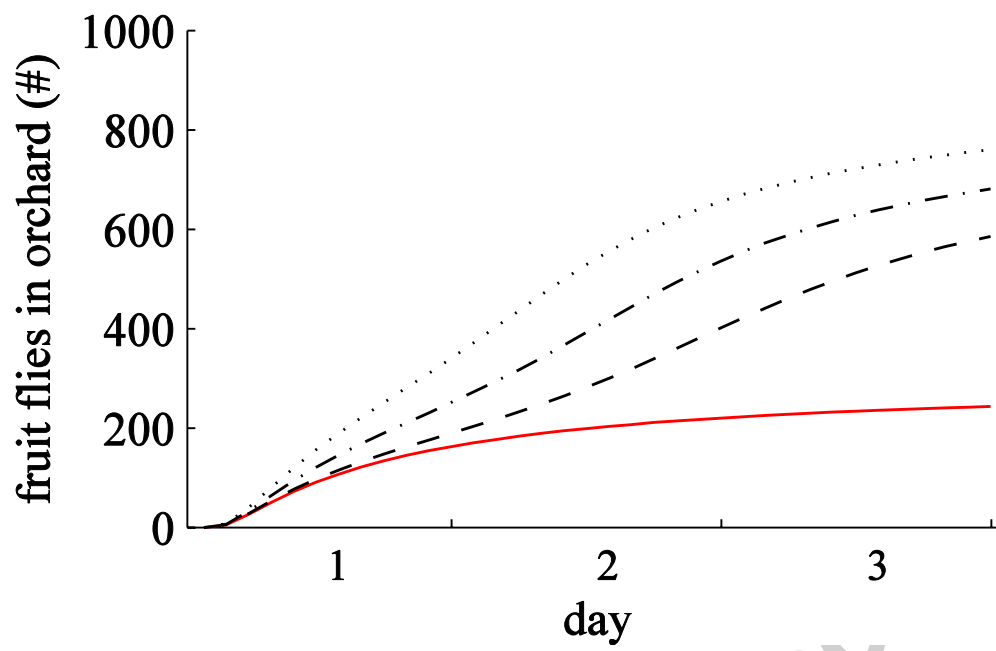
649 Figure 1:



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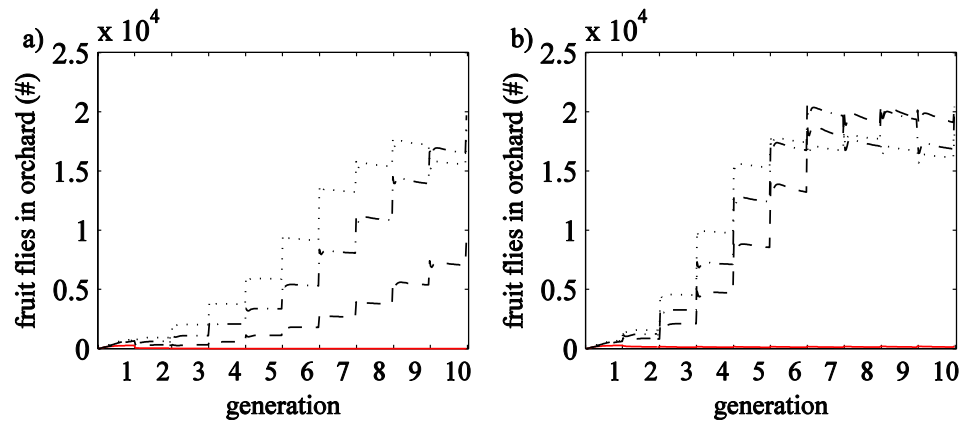
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651 Figure 2:

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653 Figure 3:

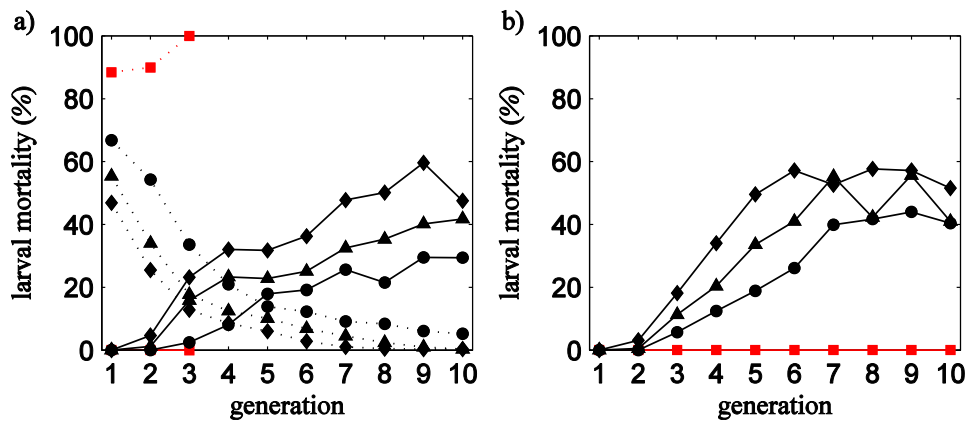


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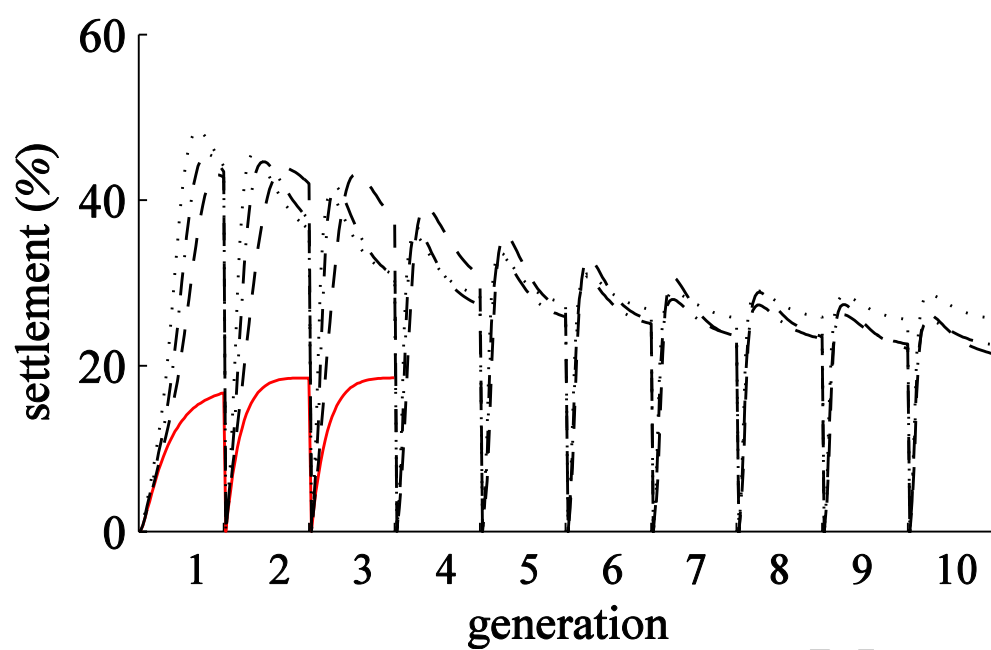
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655 Figure 4:

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657 Figure 5:



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