DISPERSAL MAY ENABLE PERSISTENCE OF FRUIT FLIES SUFFERING FROM THE ALLEE EFFECT AND SCRAMBLE COMPETITION

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Keywords: Allee effect, *Drosophila melanogaster*, establishment, extinction, scramble competition, spatial heterogeneity

Summary

Larvae of drosophilid fruit flies experience an Allee effect: they cannot develop into adults at low densities. In addition, the larvae suffer from a scramble type of competition. The Allee effect and scramble competition create a lower as well as an upper bound to the number of larvae that can successfully develop on a resource. The common resources for drosophilid fruit flies are ephemeral and patchily distributed. Therefore, a non-dispersing fruit fly population is doomed to go extinct, because the population number almost certainly crosses the lower or upper bound at some point in time. Our study shows that dispersal is one of the mechanisms that might help to surmount these effects and ensure long-term persistence of the fruit fly population.

INTRODUCTION

Many insects that exploit patchy resources are not distributed randomly (*i.e.* described by a Poisson distribution) over all available resources, but have an aggregated or clustered distribution. This behaviour is often caused by aggregation pheromones, *i.e.* substances excreted by individuals that induce aggregation behaviour in conspecifics. Rarely is this clustering investigated from a functional perspective, but it is usually just assumed that such behaviour has been selected by an Allee effect (Allee 1931): populations experience a decreased per capita growth rate at low densities. This effect can be caused by difficulties in, for example, mate finding, resource exploitation (*e.g.* overcoming host resistance) and predator avoidance or defence (Wertheim *et al.* in preparation). In drosophilid fruit flies several such mechanisms could lead to an Allee effect. We assume here that the Allee effect is only caused by larval resource exploitation in the following way. Adult fruit flies breed in ephemeral substrates in which they deposit both eggs and some micro-organisms like bacteria and yeast. These micro-organisms develop on the substrate and constitute the main larval food source. We hypothesise that adult flies in low numbers are incapable of introducing sufficient numbers of micro-organisms to render a substrate into a fermenting larval resource. Furthermore, larval activity itself might improve yeast development through tunnelling and defecation activities. Low larval densities may therefore be insufficient to cultivate the resource.

There is a negative side to clustering: severe competition within aggregations may also lead to lower population growth rate. Competition for food, space and mates can take place in all life stages and ranges between contest and scramble type. In drosophilid fruit flies competition occurs mainly in the larval stage. Larvae are confined to a single substrate until the completion of their development, and often experience severe competition for food (Grimaldi & Jaenike 1984; Sevenster 1992). Since this competition is purely of the scramble type (*i.e.* each individual takes all the bites it can without any resource defence), either all individuals are able to complete their development or none.

Thus Allee effect and scramble competition set lower and upper bounds to the number of eggs that can successfully develop within a resource item. With a model study we will investigate the effects of these bounds on population dynamics in a spatially structured environment. Non-dispersing fruit fly populations are doomed to go extinct if subject to an Allee effect and scramble competition, even if new resources are available at the same spot in each generation, because the local population number (almost) certainly crosses the lower or upper bound at some point in time (see Appendix I). In nature, however, dispersal occurs frequently in environments with patchily distributed ephemeral resources. After emergence of adult fruit flies, substrates which only last one generation are no longer available for oviposition; hence these adults must find new breeding sites. To assess its effect on persistence of a spatially distributed population, we include dispersal of the adult females in our model. The combined effects of an Allee effect, scramble competition and dispersal on population dynamics are largely unexplored, although some theoretical work exists in one spatial dimension (Kot *et al.* 1996; Lewis & Kareiva 1993).

The main goal of this paper is to investigate whether adult dispersal can lead to stable population dynamics of fruit flies in an environment where an Allee effect and scramble competition within resource items determine the window of larval survival. For this purpose we use a spatio-temporal simulation model which is parameterised for *Drosophila melanogaster.*

OUTLINE OF THE MODELLING PROCEDURE

We modelled the fruit fly population in a two-dimensional environment in 20 discrete generations, each of which consists of three steps (*i.e.* days) of dispersal by adult females and one larval development step. After each dispersal step only those (female) adults which are on resource items deposit eggs. The cumulative number of eggs on each resource item after three dispersal steps determines whether larvae will develop successfully: all larvae in one substrate survive when their number lies between the lower bound set by the Allee effect and the upper bound set by scramble competition; otherwise, all larvae die. We assumed that the surviving larvae have a sex ratio of 0.5; therefore, half of them constitute the next ovipositing adult population.

We assumed dispersal to be random, described by a two-dimensional normal distribution with zero mean and variance $\sigma^2 = 25\ \mathrm{m}^2$. This value is based on Timofeef-Ressovsky & Timofeef-Ressovsky 1940a and Timofeef-Ressovsky & Timofeef-Ressovsky 1940b who report that *D. melanogaster* moves 10 m or less per day. We computed daily dispersal as a convolution of this normal distribution and the population distribution as in Allen *et al.* 1996 and Brewster *et al.* 1999. We used apples as the resource for larval development. One apple can support development of at most 200 to 300 *D. melanogaster* larvae (Spencer 1950), so we set our upper bound at $L_{\mathrm{max}} = 250$ larvae. For the lower bound no specific estimate is available in the literature, but high mortality is found at low larval densities by Sang 1956. Therefore we (arbitrarily) chose $L_{\mathrm{min}} = 25$ larvae per apple. The daily fecundity we set at $f = 7$ (Boulétreau 1978).

We defined a grid (128 m by 128 m) with periodic boundaries: fruit flies that leave the grid on the left (or upper) side, re-enter at the right (or lower) side and vice versa. In this grid we placed initial distributions of apples and of adult female flies; from hereon we refer to the adult females simply as adults. Each gridpoint of 1 m by 1 m can contain just one resource item or none.

Because persistence in a spatial environment may depend on the resource distribution, we used different initial apple distributions representing different levels of spatial heterogeneity: (1) *Spatially homogeneous*: Apples are present at every grid point. (2)

Spatially structured: Apples are present only in specified patches in a 120 m by 120 m grid; this creates a border of 4 m on all sides. We chose patches of (A) 8 m by 8 m, with interpatch distances of 0, 2, 4, 7, 12, 16, 22, 32 and 52 m, (B) 16 m by 16 m with interpatch distances of 4, 8, 14, 24 and 44 m, (C) 24 m by 24 m with interpatch distances of 6, 16 and 36 m, and (D) 32 m by 32 m with interpatch distance 28 m spread out evenly over space. As the interpatch distances decrease, the corresponding number of patches obviously increases. The total amount of resource differs considerably between all these configurations, but note that the total amount of cells filled with resource is 4096 for 4 patches of 32 m by 32 m with interpatch distance of 28 m, 16 patches of 16 m by 16 m at distance 14 m, and 64 patches of 8 m by 8 m at distance 7 m. After each generation apples were replaced in the configuration of the initial distribution.
Persistence in a spatial environment may also depend on the initial adult distribution, so we used four different initial adult distributions: (I) *Homogeneous*: Adults present at every grid point. (II) *Point source*: Adults present in a single cell (1 m by 1 m) in the centre of the grid. (III) *4-Point source*: Adults present in four cells (2 m by 2 m) in the centre of the grid. (IV) *256-Point source*: Adults present in a 16 m by 16 m patch in the centre of the grid. In cases (II), (III) and (IV) we varied the initial number of female flies in each cell, P_0, from half of the lower bound to half of the upper bound, *i.e.* between 12.5 and 125 with steps of 12.5. In case (I) the upper bound is always immediately exceeded with these values, because with a homogeneous initial adult distribution the total number of eggs deposited in *each* resource item is approximately P_0 times 21 eggs (3 days of 7 eggs per day). To circumvent this problem we varied P_0 in this case between 2.5 and 25 with steps of 2.5.
The output variable we recorded was the total female population size for each time step. From the total population size we could then infer the number of extant generations, and thus measure whether the population could establish or not.

RESULTS

Our simulations showed that dispersal is essential for persistence of a fruit fly population both in spatially homogeneous and spatially structured environments as expected (see Appendix I): without dispersal all populations went extinct within a few generations. With dispersal the general conclusion from the simulations of all combinations of initial distribution of adult *D. melanogaster* and distribution of resources is: the initial distribution of adults determines whether a population can establish (*i.e.* produce a second generation), while the distribution of resources is mainly responsible for ultimate persistence. A point source as initial adult distribution (II) fails to establish a population in all environments irrespective of the resource distribution because the total initial adult numbers are too low; the critical number of eggs to surpass the lower boundary is not reached in any of the resource items. Similarly, low P_0 for a 4-point source adult distribution (III) and high P_0 for a homogeneous adult distribution (I) result in egg distributions outside the range (L_{min}, L_{max}) on all resource items, and these populations thus fail to establish. In every situation where the *D. melanogaster* population can establish and persist for at least several generations, all initial adult distributions lead to a qualitatively similar dynamical pattern of the total population size. Yet, population dynamics in each grid cell are highly variable and inherently unstable as can be seen in Figure 1 and Figure 2; overall stable population sizes can only be attained by local extinction and recolonisation processes.

Homogeneous resource distribution

A homogeneous initial distribution of adults (I) is doomed to extinction for all P_0 in a homogeneous resource distribution (see also Appendix I). Even though small initial populations (low P_0) can establish for one generation, persistence is never reached. A small initial local population as in cases (III) and (IV), however, can establish and persist if initial numbers of adults are sufficiently large. When the total number of adult fruit flies levels off (see Figure 1 for an example), the average number of adults per resource is about 20. Over grid cells the variation in adult number per resource item is large: many resources are not occupied and many are heavily overexploited.

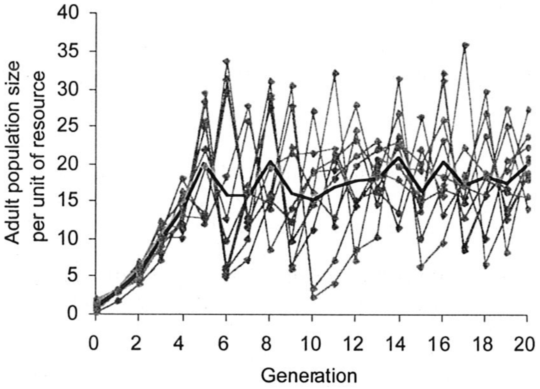

Figure 1. The development of the adult population size divided by the total number of resource items during 20 generations for different values of P_0 (grey lines) the average of which is given by the black line. The initial adult distribution is the 256-point source (IV) and the resource distribution is homogeneous (1).

Spatially structured resource distribution

For an example of a spatially structured environment, an initial adult distribution and the resulting population dynamics in such an environment we refer to Figure 2.

Some of the homogeneous initial distributions of adult *D. melanogaster* (I) and some of the local adult distributions ((III) and (IV)) can establish in an environment with a spatially structured resource, again depending on P_0. Whether populations persist depends on P_0 and on the interplay between patch size and interpatch distance. Interpatch distances of 12 m can be bridged, but from 16 m onwards other islands of resource are not attainable in sufficient numbers (see Figure 3).

It appeared that a resource patch of 32 m by 32 m is only just too small to sustain a stable population whereas the homogenous grid was large enough. Only in a situation where patches are close or large enough can a long-term global persistence of populations be achieved. In our spatially structured simulations the patches were never sufficiently large to allow for persistence without connectedness to other patches. The value at zero interpatch distance is somewhat larger than 20, the value that would be expected from Figure 1, because here a small edge of the grid does not contain resource, whereas in Figure 1 it does.

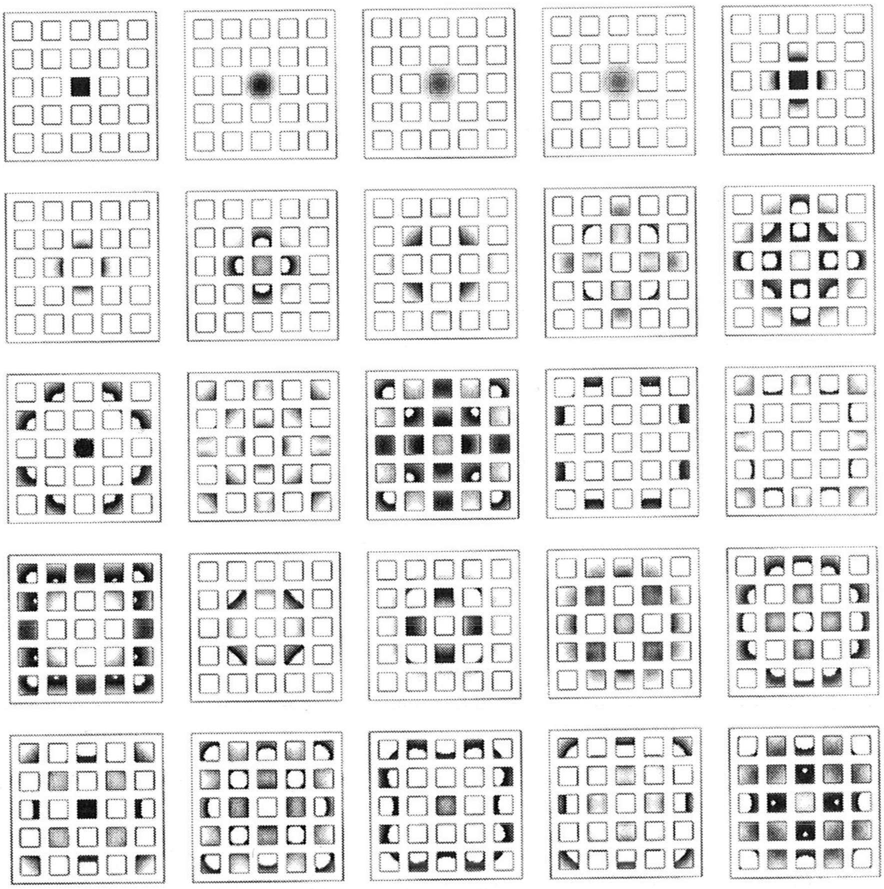

Figure 2. Snapshots of simulation results of the 256-point source (IV) in a spatially structured environment (2) of 16 m by 16 m patches at interpatch distance of 8 m, and $P_0 = 125$. The darker shades denote higher adult female fruit fly density. The first snapshot is the initial adult distribution (IV). The next three snapshots are the three dispersal steps directly following this initial distribution. The fifth snapshot shows the cumulative number of eggs after three dispersal steps. The sixth snapshot shows the resulting new generation of fruit flies that were able to overcome the Allee effect and scramble competition. The other snapshots are taken at the same point during the following generations: right after the fruit flies come out of the apples (i.e. right before dispersal).

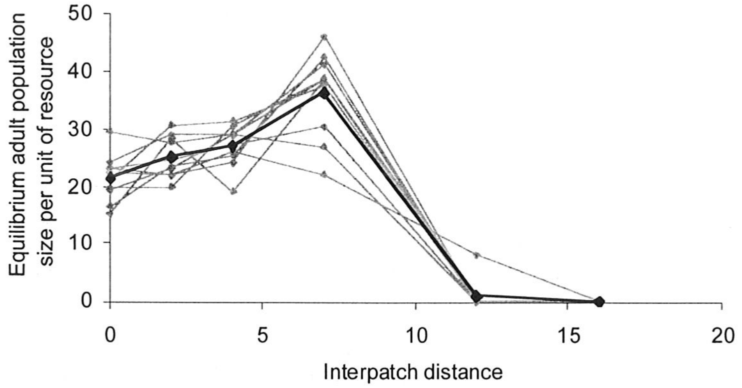

Figure 3. The equilibrium level of the adult population size per unit of resource (i.e. its value at generation 20, see Figure 1) versus interpatch distance for several values of P_0 (grey lines) the average of which is the black line. The initial adult distribution is the 256-point source (IV) and the resource distribution is spatially structured (2) with patches of 8 m by 8 m.

DISCUSSION

We have shown that dispersal is essential for persistence of a fruit fly population, where larval survival in resource items is bounded by an Allee effect and scramble competition. For dispersal to ensure persistence, some form of heterogeneity is needed, either in the resource distribution, the initial adult distribution or both. The interplay between patch size, interpatch distance and average dispersal distance further determines the fate of the population. The model presented here was inspired by the biology of *Drosophila* fruit flies, but possibly applies equally to many insects suffering from an Allee effect and scramble competition.

The simulations have been done in an environment with periodic boundary conditions, which has its advantages and disadvantages. Periodic boundaries make modelling easy, but are not entirely realistic. Using periodic boundaries is permissible for a closed system in which immigration and emigration cancel each other: all *Drosophila* that leave the simulated area are replaced immediately by immigrating counterparts. Other boundary conditions will be investigated in a future paper.

In the homogeneous initial adult distribution we had to reduce the P_0 below half the lower bound set by the Allee effect to enable establishment. This starting condition can never emerge from the simulation model itself and thus seems to contradict our assumptions. Yet it can represent a more complex situation, such as *Drosophila* being already present in the environment (*e.g.* on other resources or emerging from diapause), and then switching to apples in low densities.

As we found dispersal to be essential for persistence of a population, it will be exciting to explore various modes of dispersal in different spatial environments. This will be the subject of a forthcoming paper.

ACKNOWLEDGEMENTS

We are grateful to Hans Heesterbeek, Johan Grasman and Marcel Dicke for commenting on an earlier version of the manuscript. Martin Boer, Marco Bink, Margriet Hendriks and Hans Heesterbeek were so kind to allow us to use their computers for the simulations. We would also like to thank the National Science Foundation (INT-9813421) and the

C.T. de Wit Graduate School for Production Ecology of Wageningen University for supporting James Powell during a visit to the Netherlands.

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APPENDIX I

Essentially, when considering the system as homogeneous in space, the governing equation for the larval population L from generation n to generation $n + 1$ suffering from an Allee effect and scramble competition is given by

$$L(n+1) = g(L(n)) = \begin{cases} 0 & \text{if } L(n) < L_{\min} - \varepsilon_1 \\ fL_{\min}\left[\frac{L(n) - L\min + \varepsilon_1}{\varepsilon_1}\right] & \text{if } L_{\min} - \varepsilon_1 \leq L(n) < L_{\min} \\ fL(n) & \text{if } L_{\min} \leq L(n) < L_{\max} \\ fL_{\max}\left[\frac{L(n) - L\max - \varepsilon_2}{\varepsilon_2}\right] & \text{if } L_{\max} \leq L(n) < L_{\max} + \varepsilon_2 \\ 0 & \text{if } L(n) \geq L_{\max} + \varepsilon_2 \end{cases}$$

where f is fecundity and ε_1 and ε_2 are variables describing the range of larval densities in which the probability of survival switches from 0 to 1, respectively 1 to 0 (see Figure 4). The L_{min} is determined by the Allee effect, while scramble competition sets the upper bound L_{max}. The steady–state solution L^* is defined to be the solution to the problem $L^* = g(L^*)$ (see Edelstein-Keshet 1988). In a graphical representation this means that intersection points of the 45 degree line ($L(n + 1) = L(n)$) and the graph of $g(L(n))$ represent the steady-state solutions. As can be seen in Figure 4 there are two steady-state solutions for this problem: $L_1^* \in (L_{\text{min}} - \varepsilon_1, L_{\text{min}})$ and $L_2^* \in (L_{\text{max}}, L_{\text{max}} + \varepsilon_2)$. In general, steady-state solutions are stable if the absolute value of the derivative of the function in the steady-state solution is less than 1:

$$\left|\frac{dg}{dL}\right|_{L=L^*} < 1.$$

From experience (Bakker, 1961) it follows that ε_1 and ε_2 are such that

$$\left.\frac{dg}{dL}\right|_{L=L_1*} > 1 \text{ and } \left.\frac{dg}{dL}\right|_{L=L_2*} << -1,$$

so these steady state solutions are both unstable, Therefore, the population of *Drosophila* larvae is doomed to extinction in the spatially homogeneous case.

For simplicity we took the limit as $\varepsilon_1 \downarrow 0$ and $\varepsilon_2 \downarrow 0$ in our simulations.

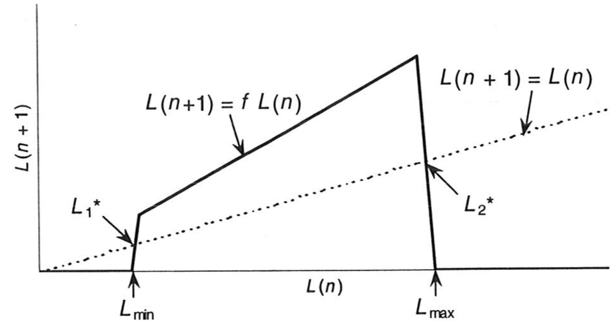

Figure 4. The larval population in one generation is the fecundity times the larval population in the most recent generation. For a larval population size below L_{min} and above L_{max} no larvae survive due to the Allee effect and scramble competition respectively. Equilibria occur where the $L(n + 1) = L(n)$ line crosses the curve $g(L(n))$ that defines the larval population in the next generation.