A Stage-structured Individual-based Model to Study Ecological and Evolutionary Dynamics of *Drosophila melanogaster* Populations Adapted for Larval Crowding

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Modelling Larval Stage in a Vial

Competition for food during larval stage is determined by not only larval density but also ecological factors inside a food vial such as nitrogenous waste build up (ref), diffusion of waste in the food below (ref), total food amount (ref). Thus, in order to investigate the adaptation to larval crowding, it is crucial to understand the ecology of the vial in which larval stage of Drosophila lab populations is maintained and replicating such environment during larval feeding becomes the first step in modelling the larval growth. Previous experimental studies on Drosophila in laboratory conditions, have shown the pattern of the growth of larvae, excretion of nitrogenous waste, larval feeding behavior in response to the waste excreted, development time (ref). Based on these experimental studies, I have created an individual-based model which considers feeding rate, efficiency to convert food into biomass, critical size and waste tolerance as larval trait parameters to measure other traits which are variables such body size, development time, and survivorship.

2.1 Ecology of a Vial in Drosophila Cultures

During larval feeding inside a vial, larvae are able to access only a certain amount of food from the total food available at a given time point. This is due to their inability to dig more to access food (ref), and this accessible food is referred as the feeding band. For simplicity, feeding band is taken as volume of food proportional to the diameter of the vial. In the model, I also assume this feeding band to be a constant volume of food in all types of culture vials till it reaches the bottom of the vial. The growth of larvae in the model is affected by waste build up and food quality in the feeding band. I also consider a diffusion band which is a part of the total food

below feeding band where some amount of waste can diffuse from feeding band at each time step. Fig 2.1 is the visualization of feeding band and diffusion band during larval feeding.

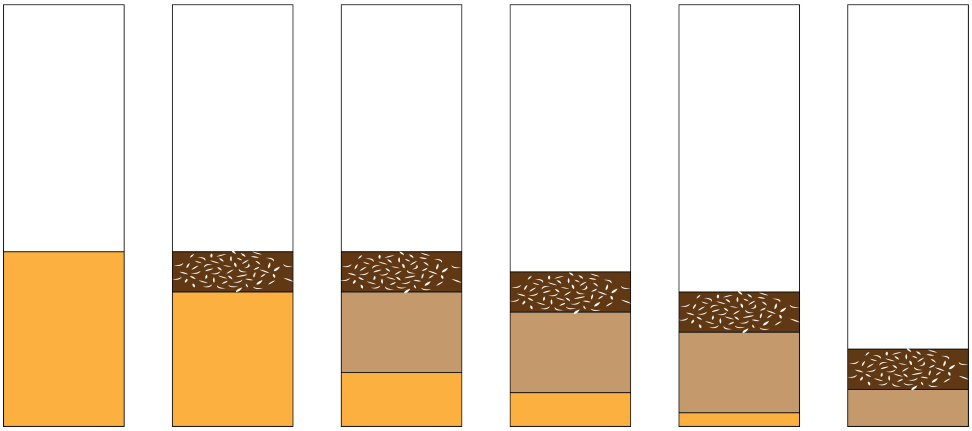

Figure 2.1: Ecological dynamics in a vial during larval feeding

2.2 Larval Stage Model

Each individual egg is assigned larval trait parameters from respective distributions with certain mean and variation (table no.). For a given amount of food and number of eggs keeping the sex ratio 1:1, the model follows certain set of rules as described in fig 2.2 which are simulated in discrete time steps. Critical size and efficiency are taken as sexually dimorphic traits and are assigned depending on the sex of the individual larva. Critical size and efficiency of females are assumed to be higher than that of males.

The inital size of all larvae is same and the growth is determined by larval trait parameters such as initial feeding rate, efficiency, waste tolerance and critical size assigned to each individual from distributions with respective mean trait value and variation. The larval growth is divided into two stages determined by whether critical size is reached or not, These stages are called pre-critical and post-critical stage.
In pre-critical stage of the larva, feeding rate is a linear function of time, given as:

$$Fr_i(t) = fr_i + x_1 \cdot t$$

Here,
fr_i: initial feeding rate of i^{th} larva; x_1: scaling parameter,
t: given time step; $Fr_i(t)$: Feeding rate at time t

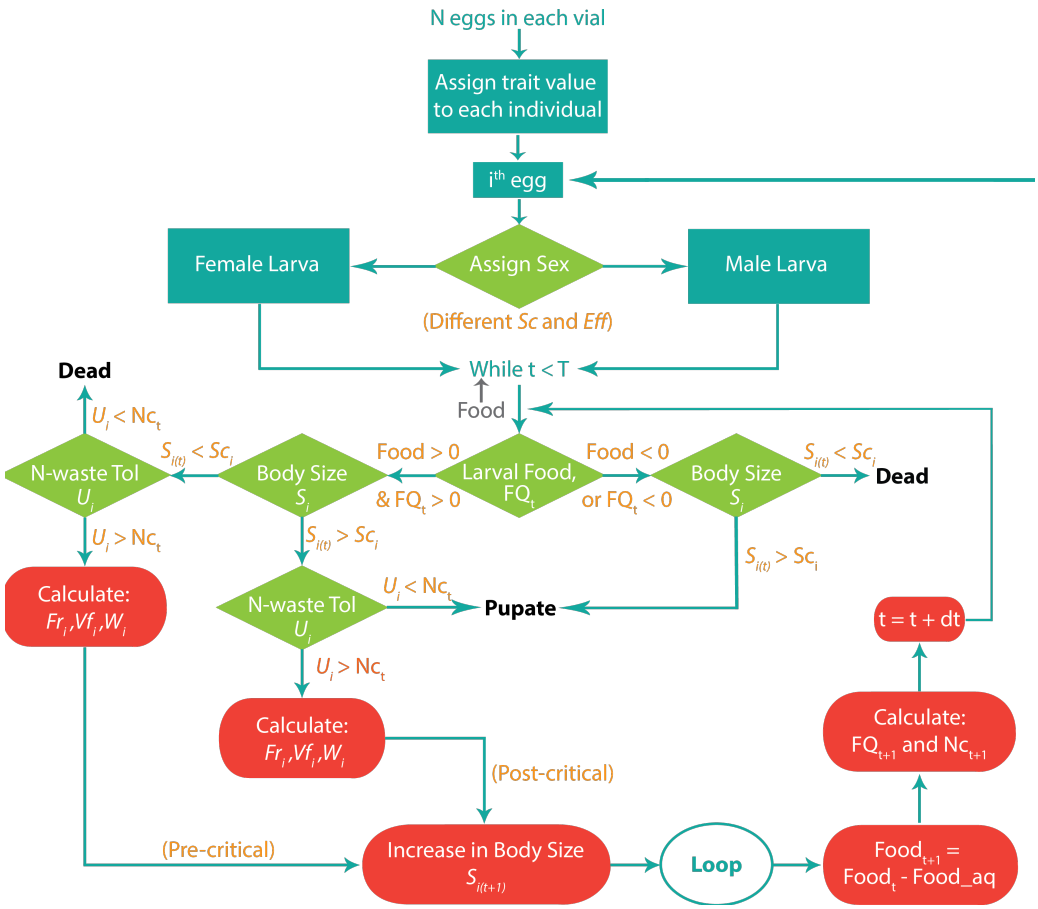

Figure 2.2: Flowchart of the larval stage in the model

Feeding rate stays constant During post-critical stage. During pre-critical growth Volume of food taken in one bite is taken as constant $V_f(pre)$ and during post-critical growth it is $V_f(post) = 1.5 \cdot V_f(pre)$. Food consumed by all larvae at time step t is given as:

$$FoodEaten(t) = \sum_i food\_eaten_i(t) = \sum_i Fr_i(t) \cdot V_f$$

The increase in body size at time t is $S_i(t+1)$ and give as:

$$S_i(t+1) = S_i(t) + food\_eaten_i(t) \cdot \epsilon_i \cdot FQ_{fb}(t)$$

Here,

ϵ_i: Efficiency to convert food eaten into biomass of i^{th} larvae,

$FQ_{fb}(t)$: Food quality of the feeding band at time t

After feeding and utilizing food consumed at given time step, larva produces nitrogenous waste $waste\_prod_i(t)$. This affects the total waste produced by all the larvae after feeding:

$$WasteProd(t) = \sum_i waste\_prod_i = \sum_i [food\_eaten_i(t) \cdot (1 - \epsilon_i \cdot FQ(t))]$$

Based on this waste produced, total waste accumulated till time step t in feeding band and diffusion band is calculated considering k_d proportion of waste in the feeding band diffuses into diffusion band at each time step.

$$Waste_{fb}(t+1) = Waste_{fb}(t) + (1-k_d) \cdot WasteProd(t) + \frac{FoodEaten(t) \cdot Waste_{db}}{dband}$$

$$Waste_{db}(t+1) = Waste_{db}(t) + k_d \cdot WasteProd(t) - \frac{FoodEaten(t) \cdot Waste_{db}}{dband}$$

Food quality of the feeding band at time step t is:

$$FQ_{fb}(t) = 1 - \frac{Waste_{fb}(t)}{fband}$$

If $FQ_{fb}(t) \leq 0$, it means that there is no food available to eat and feeding band contains only nitrogenous waste and larvae stop eating.

k_d is dependent on the food available in the vial and determines whether waste is diffused into the diffusion band. Its values are assigned at each time step as follows:

i k_d is a constant > 0 if $food > fband + dband$

ii $k_d = 0$ if $food \leq fband + dband$

Each larva feeds and increase the body size in each time step based on the conditions for food available ($food$), food quality ($FQ(t)$), critical size (sc_i) and waste tolerance (u_i) described in fig 2.2.

Values for larval trait parameters obtained from distributions as described in table (ref), were varied and calibrated to obtain survivorship, body size and development time results similar to the empirical results in various larval densities (table no.). These larval trait values represent MB-tpye (control population) larval traits.

2.3 Feeding Band Dynamics

Simulations are performed for MB-type larvae to observe the waste build up dynamics in a food vial with different larval densities during larval feeding. In fig 2.3, waste build in the feeding band throughout larval feeding at different larval densities is plotted. At low density i.e. 60 eggs / 6 ml food (MB culture), there is very little nitrogenous waste building up due to diffusion and plenty of food available below the feeding band at all time steps unlike at high densities.

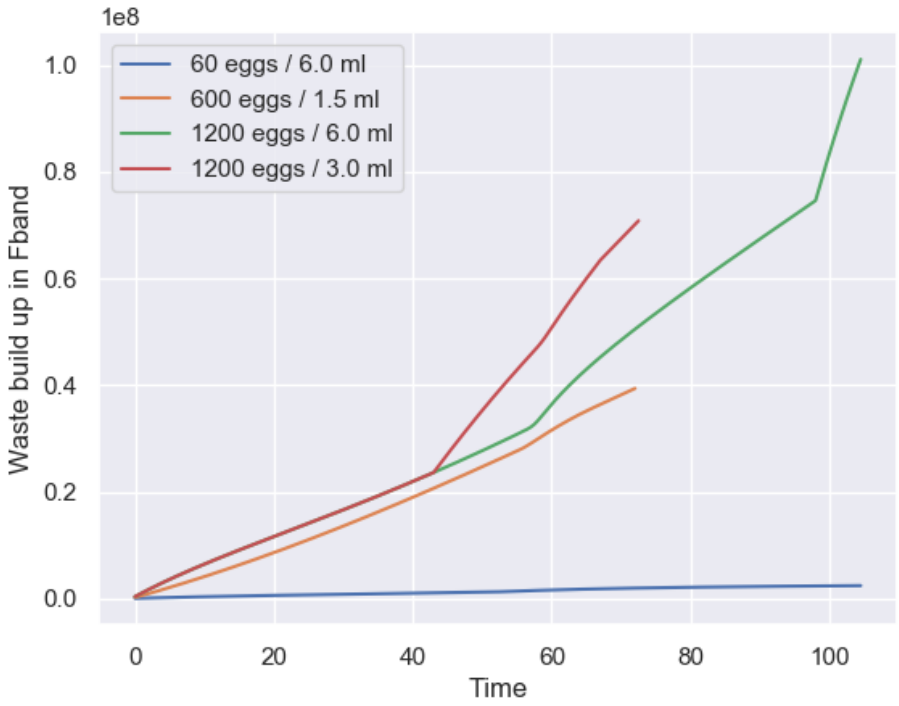

Figure 2.3: Waste build up in the feeding band

High densities - 600 eggs / 1.5 ml food (MCU culture) and 1200 eggs / 3 ml food (CCU culture) show different patterns of waste build up in the feeding band, even though total larval density is equal. This is due to differences in diffusion pattern in MCU and CCU culture vials. In MCU culture vial, there is very little food available below the feeding band, thus diffusion does not occur and waste build in the feeding band increases gradually. In CCU culture vial, waste build is almost in same qauntity as in MCU culture in earlier stage, even though effective larval density is double (number of larvae per feeding band). This is due to the availablilty

of food below feeding band in CCU culture where waste can diffuse. After approx. 40^{th} time step, diffusion stops and waste from diffusion band enters feeding band in more quantity, thus giving a sudden increase in the waste build rate.

LCU culture vial (1200 eggs in 6 ml food) also shows pattern waste build in the feeding band similar to CCU culture vial, but shows increase in the rate of waste build up at approx. 60^{th} time step as there is more food available below the feeding band compared to CCU culture vial. At approx. 100^{th} time step in LCU culture vial shows even more increase in the rate of waste build because diffusion band touches the bottom and starts shrinking.

2.4 Discussion

Time to reach critical size survivorship ccu and mcu differences

Chapter 3

Interplay between Larval Trait Parameters and Life-history Traits

In the base model of larval stage, trait parameters used are initial feeding rate, efficiency, critical size and waste tolerance. These parameters can not be measured directly via experimental approaches, but their effect on other larval traits such as body size, feeding rate at the third instar, development time can be measured easily. Here, I explore how larval trait parameters interact with each other and affect body size, time to reach critical size, feeding rate at critical size and survivorship. Since feeding rate in the model stays constant after reaching critical size, it can be taken as proxy for feeding rate at the third instar stage.

3.1 Initial Feeding Rate and Efficiency

In MB culture (low density), fig 3.1 shows having higher efficiency as well as higher initial feeding rate gives higher larval body size, but lower time to reach critical size. Feeding rate at critical size is dependent on time taken to reach critical size which is dependent on body size increment at each time step. This body size increment is proportional to the current feeding rate and efficiency. Thus, efficiency and initial feeding rate both affect the feeding rate shown at the critical size. Having lower efficiency and higher initial feeding rate tends to give higher feeding rate at critical size in MB culture. Survivorship does not show any pattern at low density, since most of the larvae are competing very less and are able to survive easily.

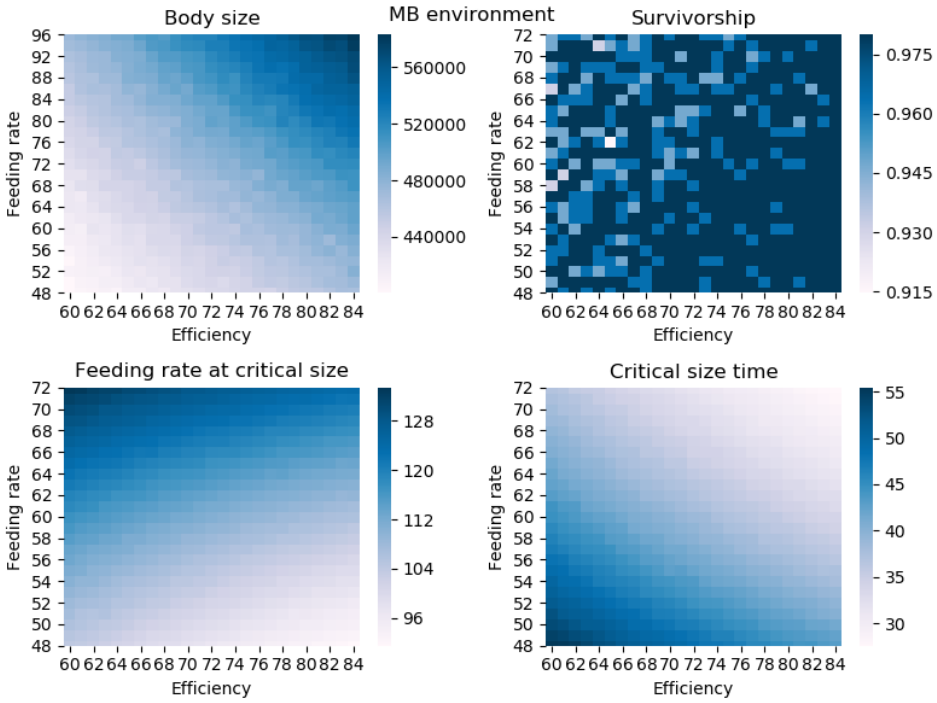

Figure 3.1: Effect of initial feeding rate and efficiency on larval traits in MB culture

In MCU and CCU cultures (high densities), fig 3.2 and fig 3.3 show that time to reach critical size show similar pattern as seen in MB culture with varying efficiency and initial feeding rate. The maxima possible is higher in high density cultures than maxima possible in low density culture, showing that it takes more time to reach given critical size at high densities than at low density with same efficiency and initial feeding rate values. Feeding rate shown at critical size also shows similar pattern as seen in MB culture but with higher maxima reached with same parameter ranges. This suggests feeding rate shown at critical size is also a density dependent trait. The complete white pixels in all heatmaps (fig 3.2 and fig 3.3) are the values where none of the larvae survived, so the trait could not be measured and are to be excluded.

At high densities, especially at MCU density, body size and survivorship are not affected by initial feeding rate, unlike at low density. Food acquired while having either higher or lesser initial feeding rate, remains almost the same. This is due to the decrease in food quality is higher for higher initial feeding rate. Thus, overall body size increment which is majorly determined by food quality at high densities, is approximately same in both cases i.e. larval growth with both higher and lower initial feeding rate. Survivorship also shows similar pattern as body size for these two parameters, since it is determined by whether critical size is reached or not.

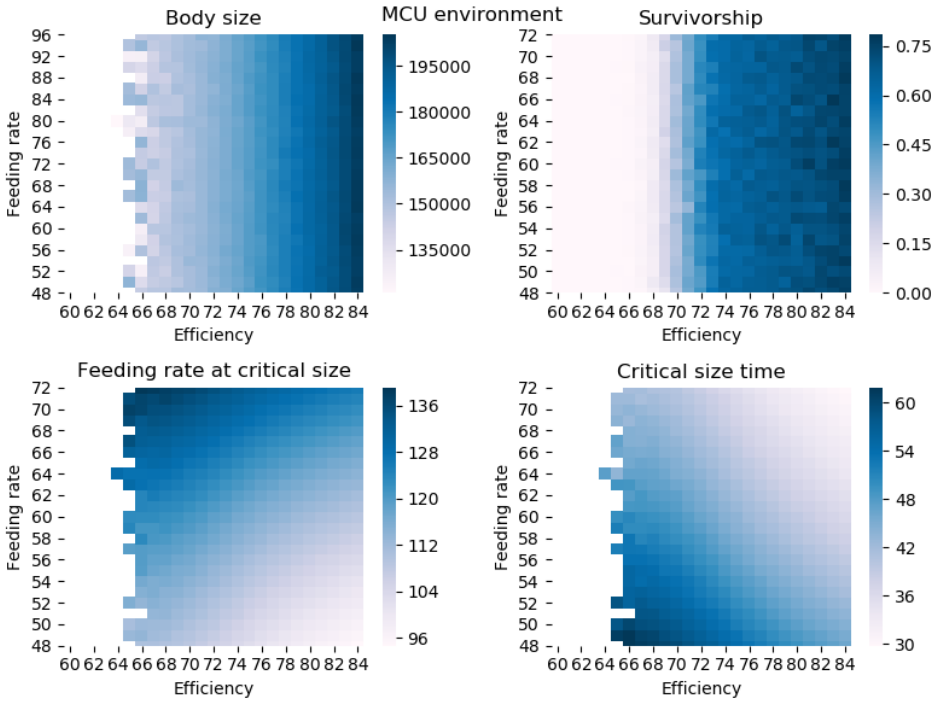

Figure 3.2: Effect of initial feeding rate and efficiency on larval traits in MCU culture

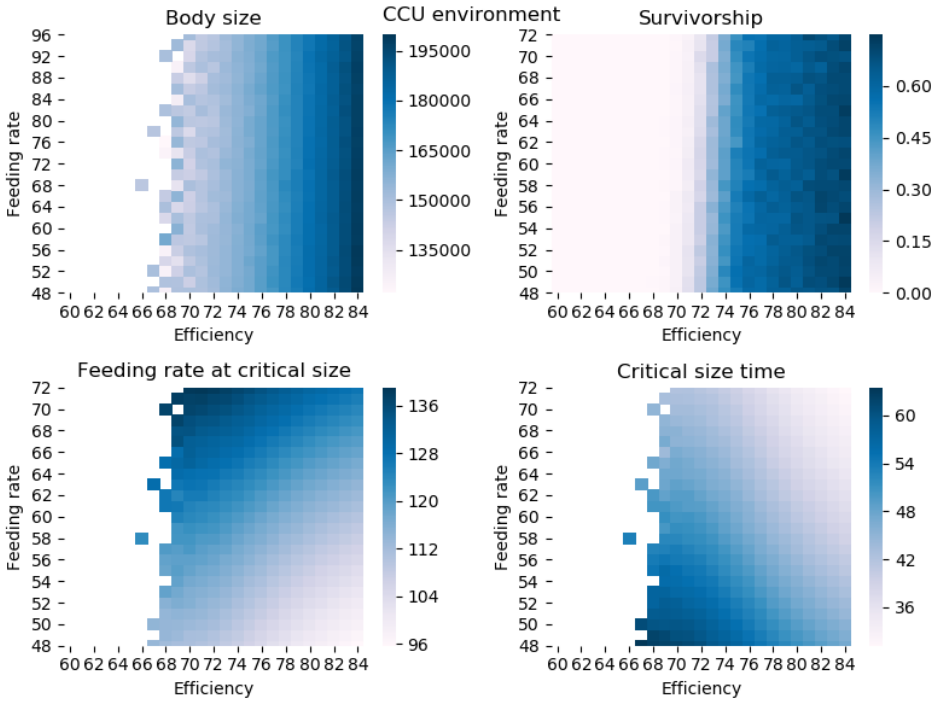

Figure 3.3: Effect of initial feeding rate and efficiency on larval traits in CCU culture

3.2 Initial Feeding Rate and Critical Size