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

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Introduction

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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.

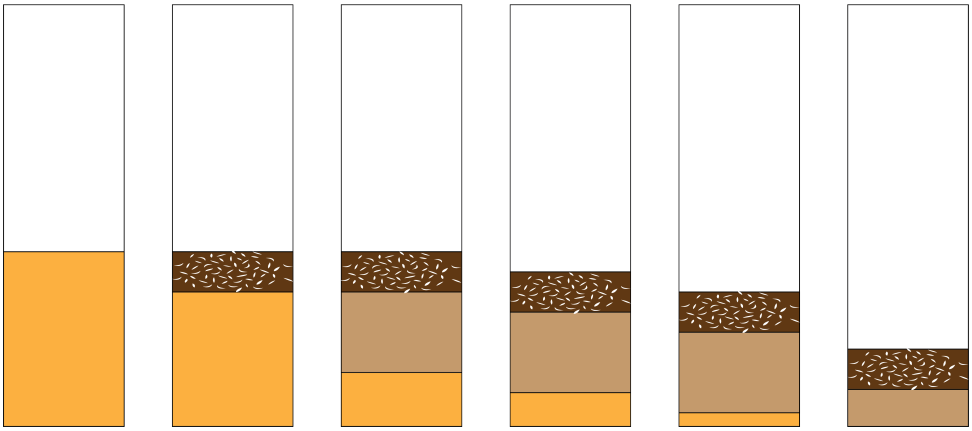

Figure 2.1: Ecological dynamics in a vial during larval feeding

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

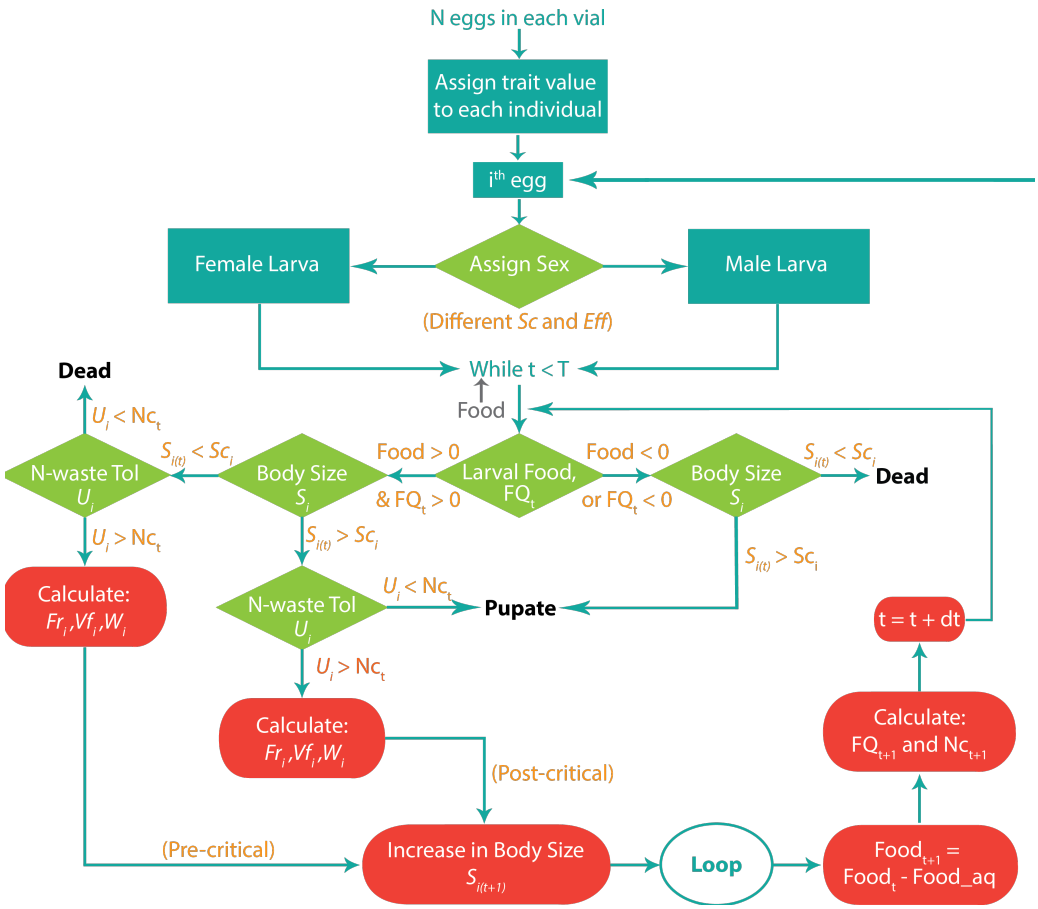

Figure 2.2: Flowchart of the larval stage in the model

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.

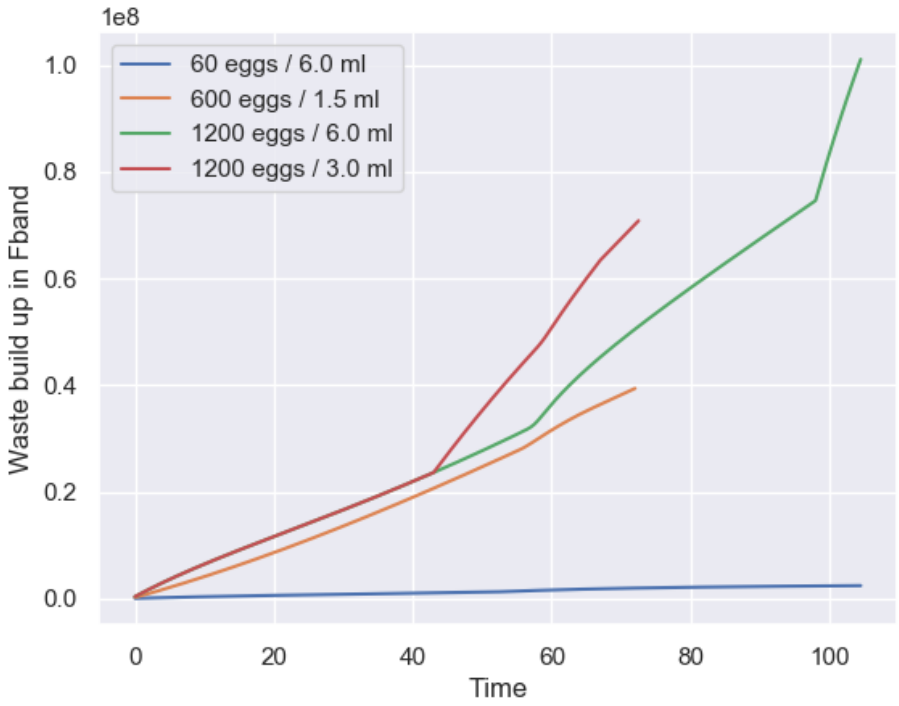

Figure 2.3: Waste build up in the feeding band

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

References

Chapter 3

Interplay between Larval Trait Parameters

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.

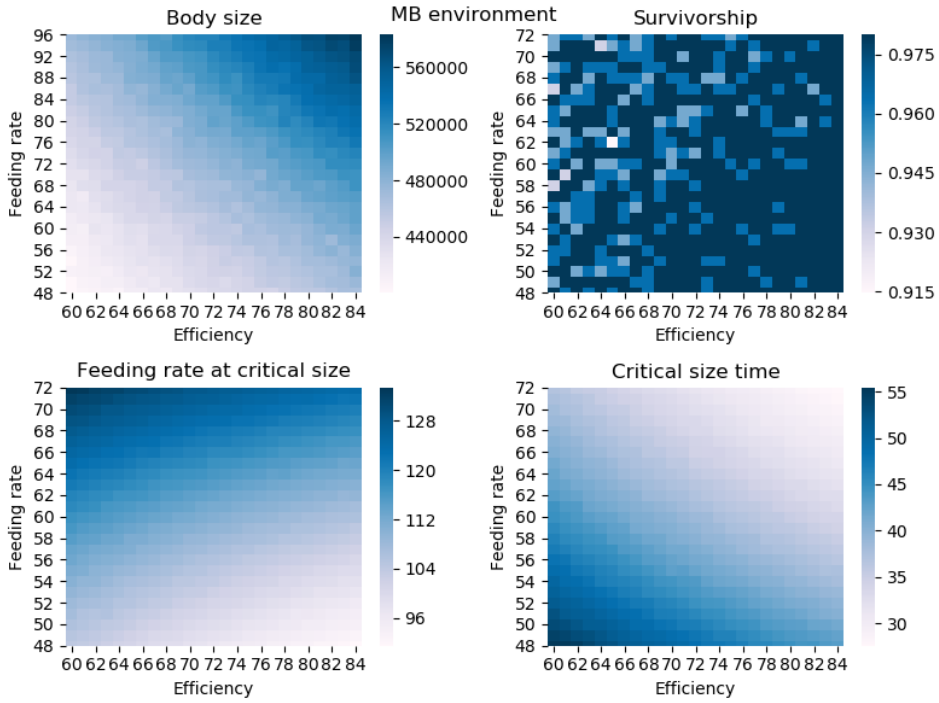

Figure 3.1: Effect of initial feeding rate and efficiency on larval traits in MB culture

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.

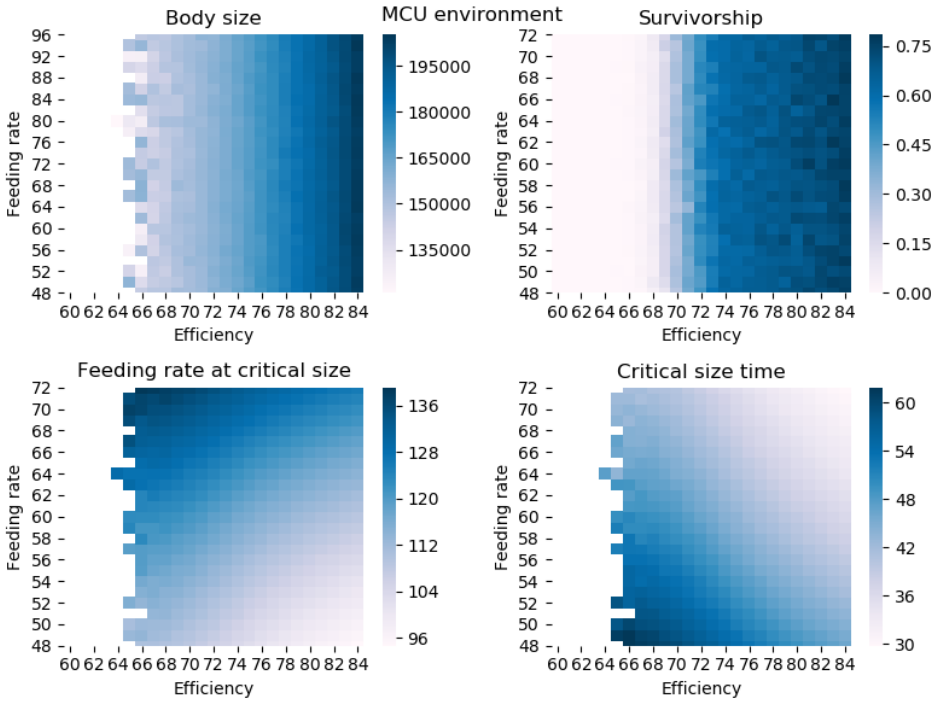

Figure 3.2: Effect of initial feeding rate and efficiency on larval traits in MCU culture

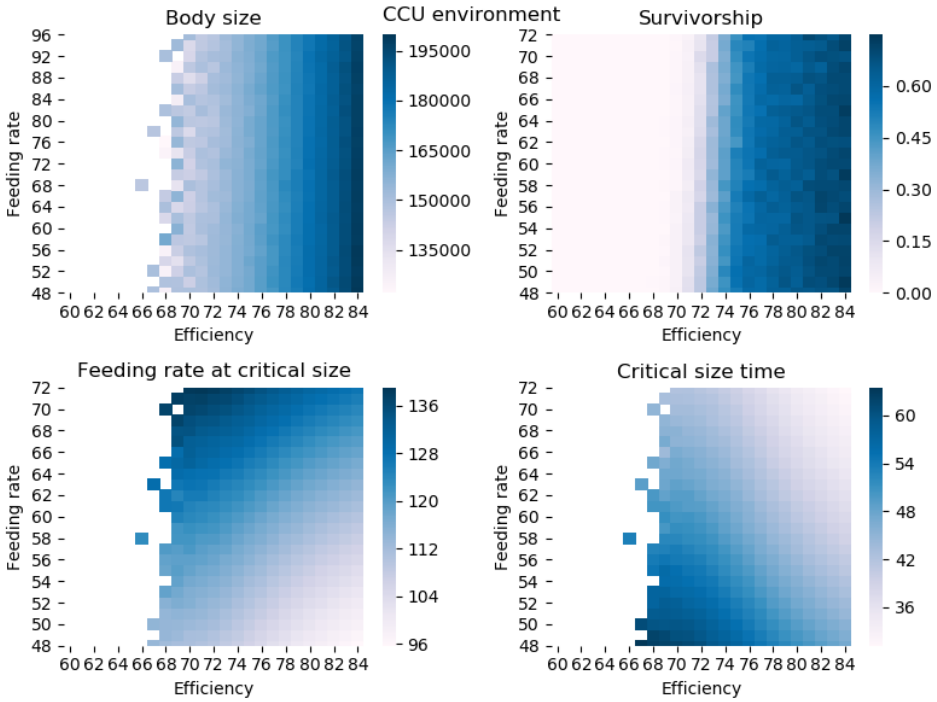

Figure 3.3: Effect of initial feeding rate and efficiency on larval traits in CCU culture

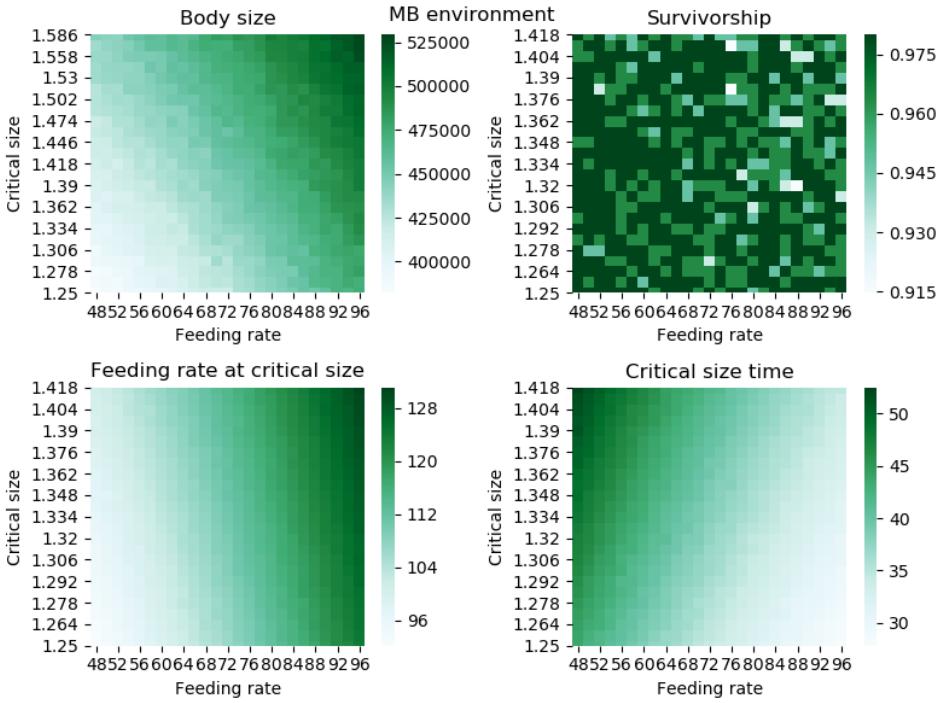

Figure 3.4: Effect of initial feeding rate and critical size on larval traits in MB culture

3.2 Initial Feeding Rate and Critical Size

In MB culture, fig 3.4 shows having higher critical size and higher initial feeding rate leads to higher larval body size. Lower critical size and higher initial feeding rate is beneficial in having lower time to reach critical size. Feeding rate at critical size is majorly determined by initial feeding rate, while having higher critical size gives slightly higher feeding rate, since time to reach critical size is more. Survivorship is not affected by either initial feeding rate or critical size at low density, since competition for food is minimal.

In MCU culture fig 3.5, body size is not affected by either critical size or initial feeding rate and post-critical growth is very less. Time to reach critical size and feeding rate at critical size show similar pattern as shown in MB culture with higher maxima for same values. Survivorship is only affected by critical size and initial feeding rate has no effect on survivoship at MCU density. Lower critical size shows trend for higher survivoship, since larvae are able to pupate in lesser time before food quality decreases drastically.

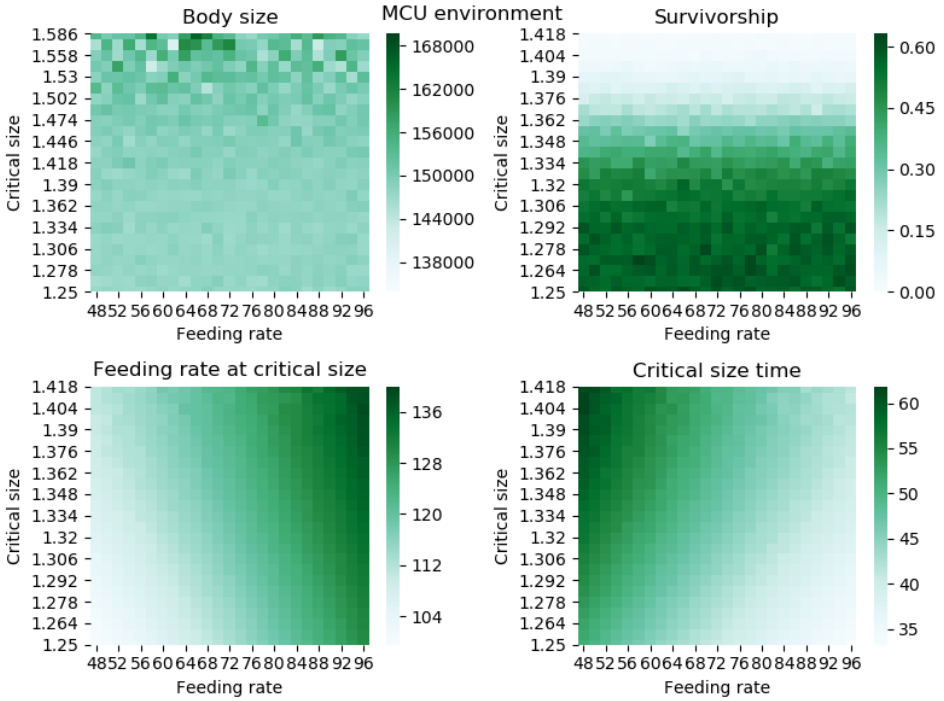

Figure 3.5: Effect of initial feeding rate and critical size on larval traits in MCU culture

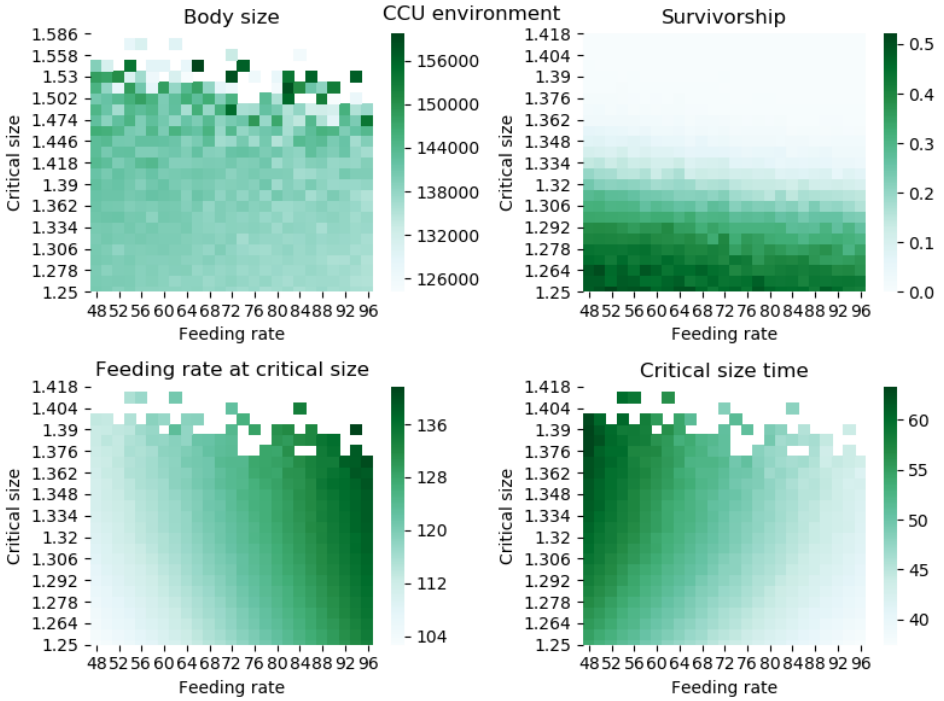

Figure 3.6: Effect of initial feeding rate and critical size on larval traits in CCU culture

In CCU culture, fig 3.6, patterns of body size, time to reach critical size and feeding rate at critical size similar to the ones in MCU culture. Survivorship shows small effect of initial feeding rate as well along with critical size. Having lesser average initial feeding rate in the population leads to slower urea build up and decrease in food quality of the feeding band, thus larvae with higher critical size are able to survive.

3.3 Critical Size and Efficiency

In MB culture, fig 3.7, shows increase in body size with increase in critical size and efficiency. Feeding rate at critical size and time to reach critical size both increase with increasing critical size and decreasing efficiency. Higher efficiency leades to decrease in critical size thus feeding rate shown at critical size reaches lesser maxima. Survivorship shiws no effect of these parameters at low density.

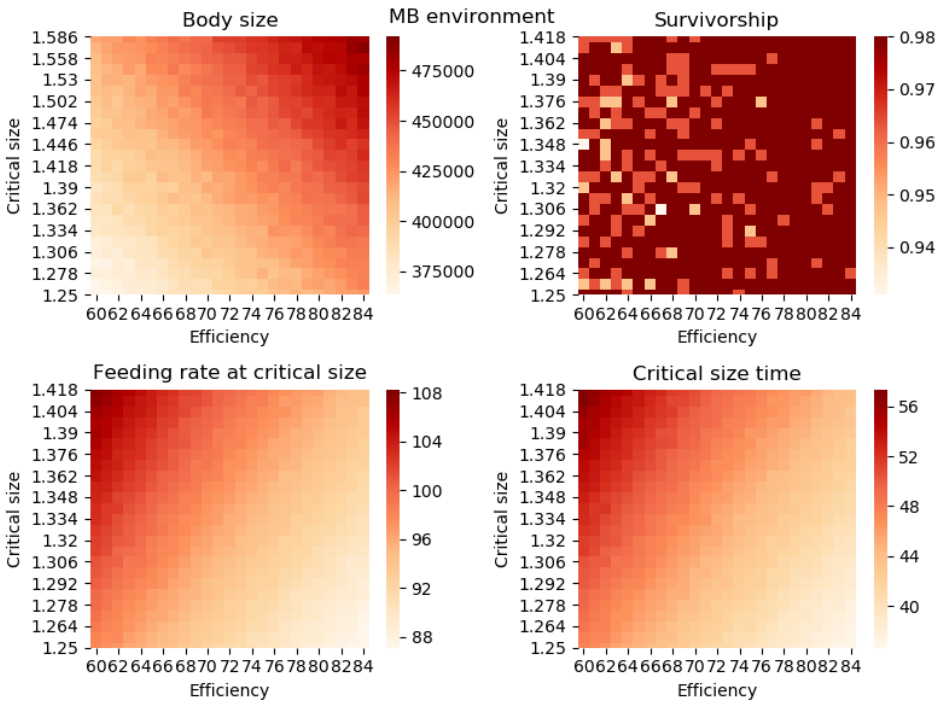

Figure 3.7: Effect of critical size and efficiency on larval traits in MB culture

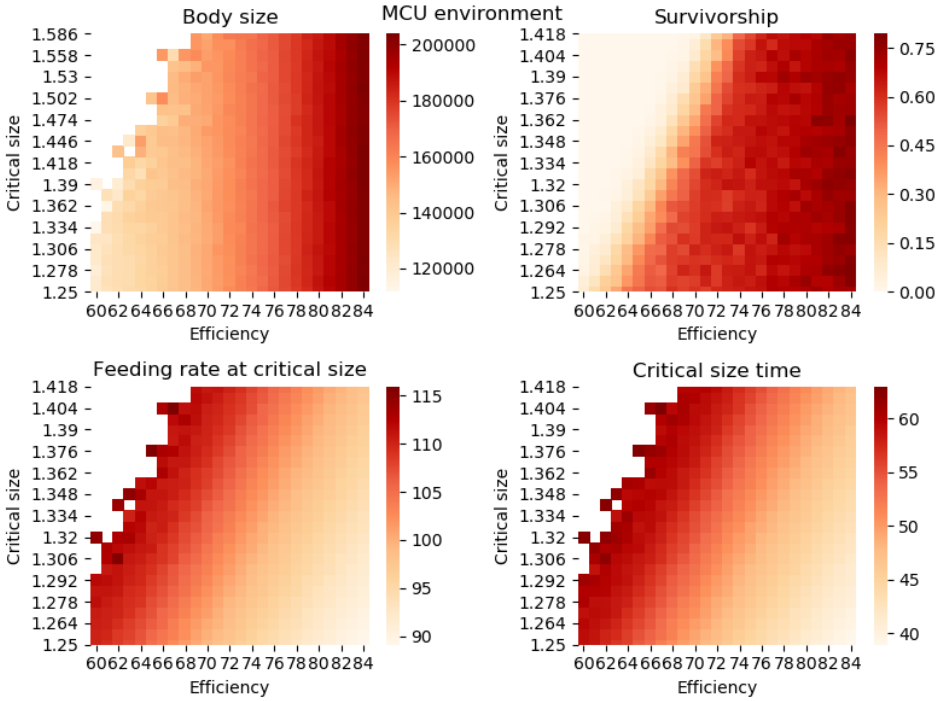

Figure 3.8: Effect of critical size and efficiency on larval traits in MCU culture

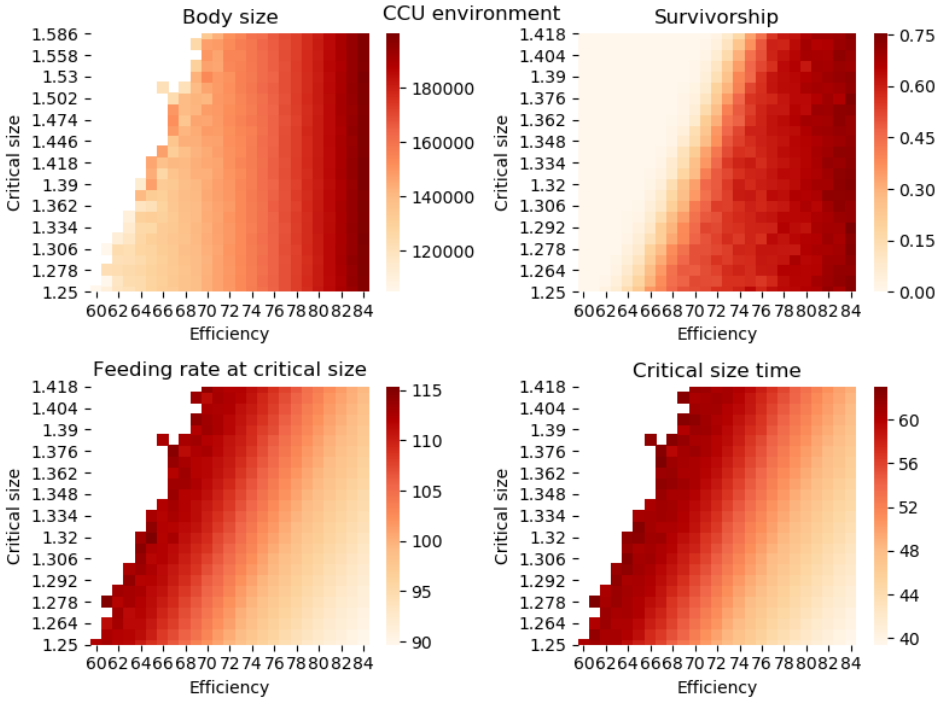

Figure 3.9: Effect of critical size and efficiency on larval traits in CCU culture

In MCU and CCU culture, fig 3.8 and fig 3.9, all the larval traits show similar pattern as in MB density with critical size and efficiency. The maxima for feeding rate at critical size and time to reach critical size is higher compared to the ones at MB density. Body size and survivoship maxima are lesser at high density.

3.4 Discussion

References

Chapter 4

Modelling Evolution of Life-history Traits

4.1 Modelling Adult Stage

After modelling larval stage and calibrating, I developed the model for the adult stage of *Drosophila* life cycle. This includes randomly choosing surviving adults from all replicate larval stage vials, matings, and inheritance of larval trait parameters from parents to offspring. Female is mated once with random male chosen from the adult population with replacement for simplicity. From all the offspring produced, eggs are chosen at random with numbers respective to the crowding environment maintained for the next generation.

4.1.1 Fecundity

After each mating, the number of eggs produced for a female are derived from the fecundity equation based on the model of (ref) Tung S. (year). Fecundity is taken as a function of body size of the female and adult nutrition parameter (the amount of yeast provided). Fecundity of an i^{th} female is given as:

$$Egg_i = Nut \cdot x_2 \cdot \log(x_3 \cdot s_i)$$

Here, s_i = body size of the i^{th} female

Egg_i = Number of eggs laid by the female in a mating

Nut = Adult nutrition i.e. the amount of yeast provided

x_2, x_3 = scaling parameters

4.1.2 Inheritance

Larval trait parameters (initial feeding rate, effieciency, waste tolerance and critical size) are inherited from parents to offspring produced by each female using mid-parent value. The mid-parent value i.e. average of mother and father for each larval parameter of offspring as mean is calculated for offspring. This mid-parent value is taken as mean of a normal distribution with fixed standard deviation. The standard deviation in this normal distribution determines the heritibility of the mid-parent value and it is considered to be different for each trait parameter. Trait parameters of the offspring are assigned as:

$$T_i \in N(mpv_T, \delta_T)$$

Here,
T_i = Trait parameter assigned to i^{th} offspring from a mating
mpv_T = Mid-parent value of of the trait T for a given mating
δ_T = Stochasticity in mid-parent value of the trait T
$N(mpv, \delta)$ = Normal distribution with mpv as mean and δ as standard deviation

4.2 Effect of Laral Crowding on the Evolution of Life-history Traits

Using initial values for all parameters given in table (no.), the entire model is simulated for 100 generations with 10 replicates for MB, MCU and CCU cultures. All larval trait parameters are taken from independent distribution and there is no correlation between them. To see how larval trait parameters evolve over time, timeseries for these traits of surviving adult individuals are plotted with 95% CI.

Initial feeding rate in high density cultures increase over generations at similar rate but inital feeding rate is higher always in CCU culture always than in MCU culture. In MB culture, being control population, initial feeding rate does not evolve (fig 4.1).

Efficiency show similar trend in high density cultures i.e. it increases over generations at similar rate but is higher always in CCU culture always than in MCU culture. In MB culture, being control population, efficiency does not evolve (fig 4.2).

Critical size in high density cultures decreases at the same rate but critical size in CCU culture is always lower than in MCU culture. In MB culture, critical size does not change over generations (fig 4.3).

Waste tolerance does not evolve in all of the culture populations since there is no significant decrease/increase in waste tolerance value (fig 4.4).

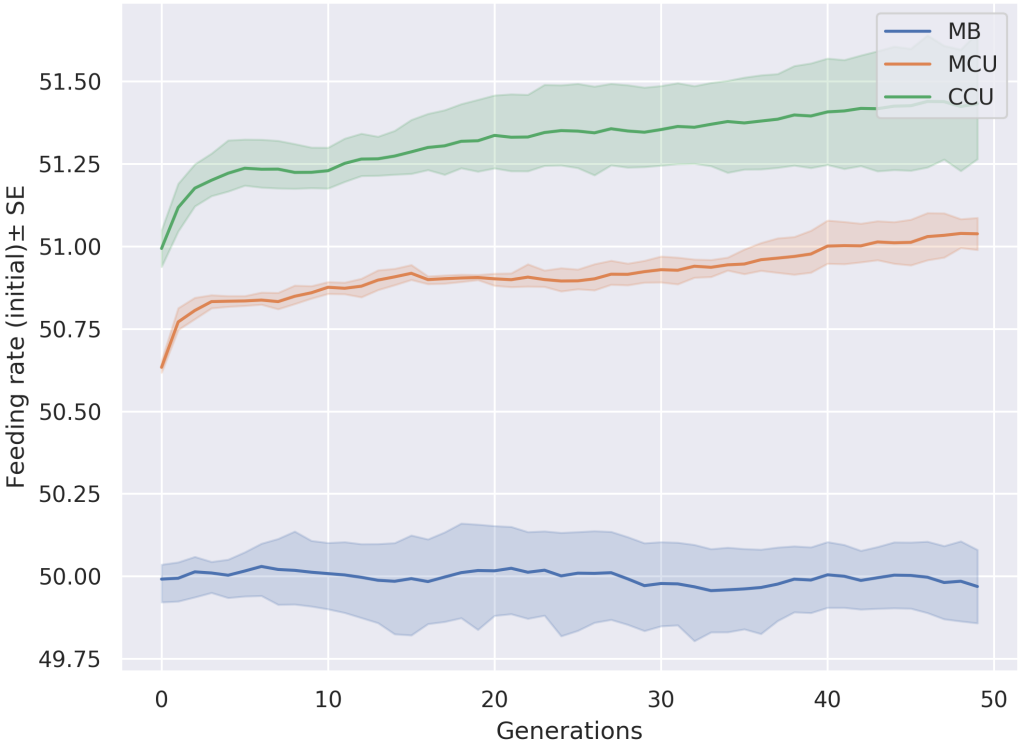

Figure 4.1: Timeseries for initial feeding rate

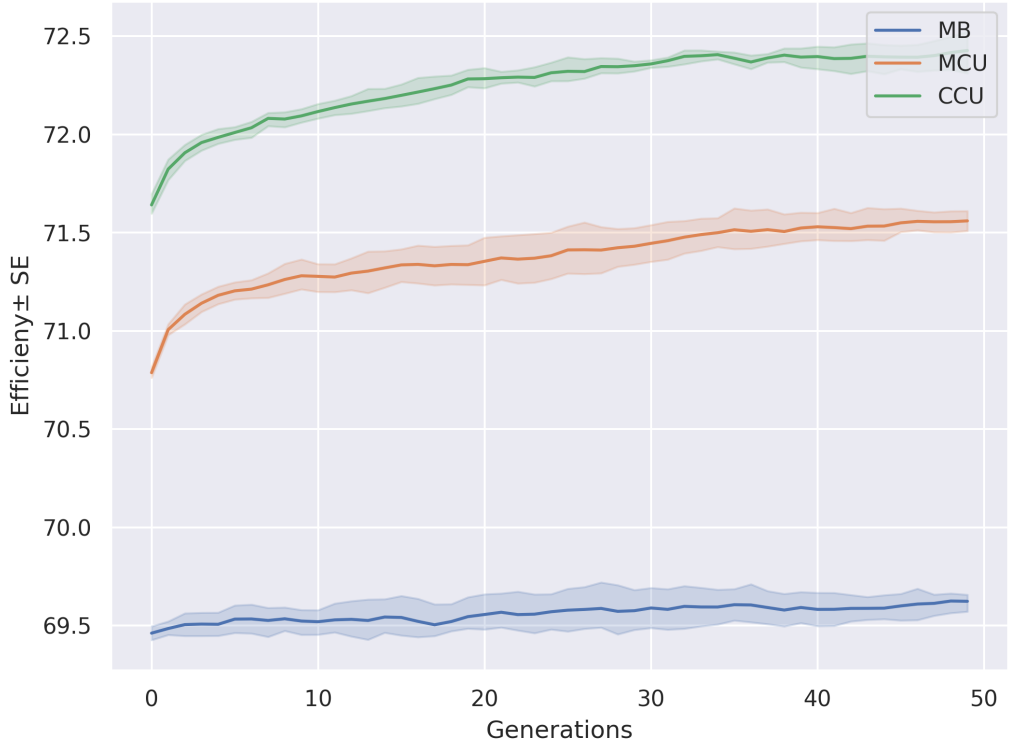

Figure 4.2: Timeseries for initial efficiency

4.3 Effects of Variation on the Evolution of Larval Trait Parameters

The source of variation in the model comes from the initial variation in the larval trait parameters, given as certain standard deviation in the respective initial distribution as well as from the heritibility of the mid-parent value during the inheritance of the larval trait parameters. The simulations show how these sources of variations play an important role in determining the evolutionary routes taken to acheive greater competitive ability by having maximum survivorship.

4.3.1 Variation in the Initial Distribution of Larval Trait Parameters

When timeseries are plotted for the larval trait parameters, the variation in the initial distribution of these trait parameters determine the maxima that can be achieved to increase the fitness. From fig(a), fig(b) and fig(c), it is seen that differences in variation of these trait values, maxima reached are different with similar initial mean trait values. If the initial variation in efficiency is very high compared initial variation in feeding rate, then feeding rate does not reach higher feeding rate after few generations unlike of the timeseries simulations performed with lower initial variation in the efficiency. Depending on the initial variation in each trait separately, traits can evolve differently, since these trait parameters interact with each other to give complex phenotypes suxh as body size, time to rach critical size and survivorship.

4.3.2 Heritibility in Mid-parent Value

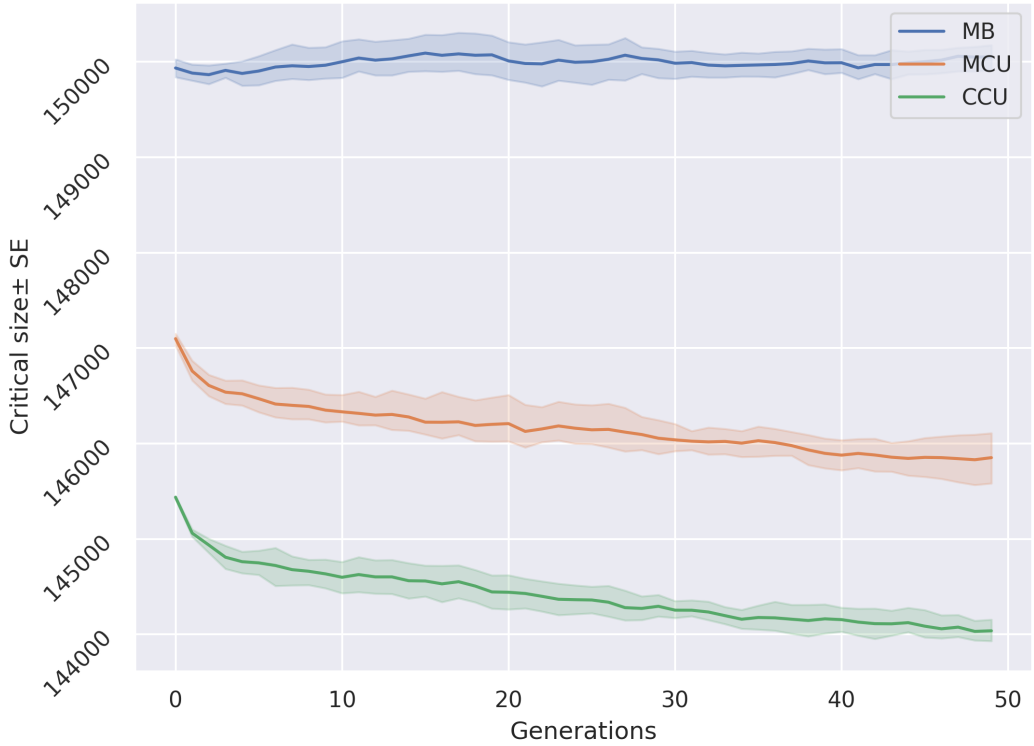

Figure 4.3: Timeseries for initial critical size

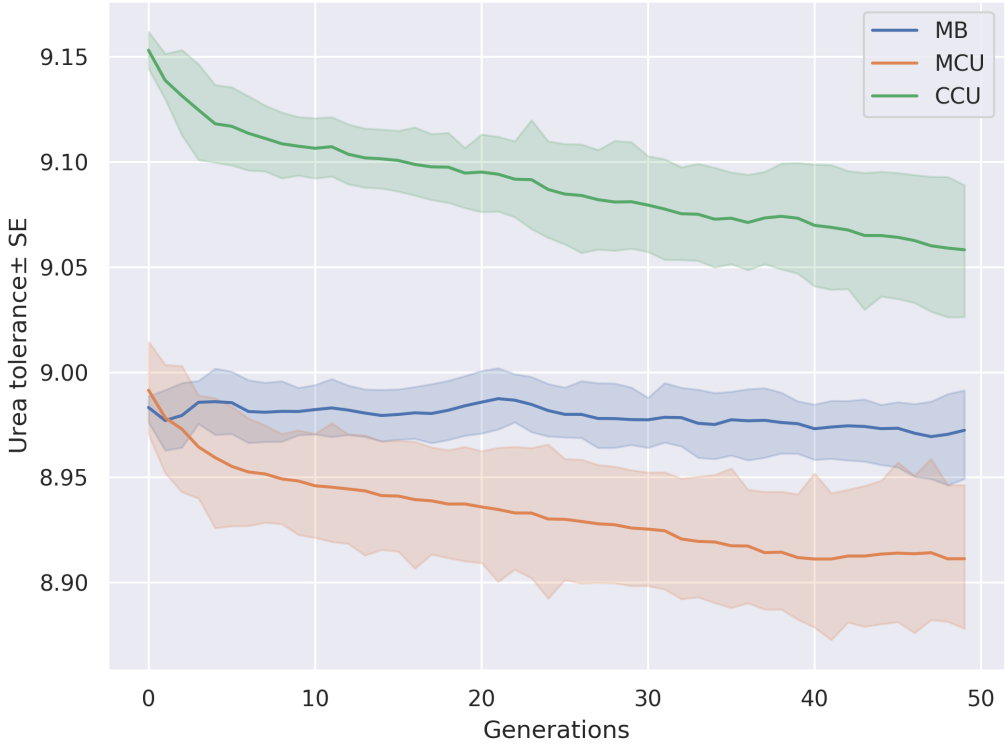

Figure 4.4: Timeseries for initial waste tolerance

References