

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

**Sayyed Imran Rashid**

*A dissertation submitted for the partial fulfilment of  
BS-MS dual degree in Science*



**IN PURSUIT OF KNOWLEDGE**

**Indian Institute of Science Education and Research, Mohali  
April 2020**

## Certificate of Examination

This is to certify that the dissertation titled “**A Stage-structured Individual-based Model for Ecological and Evolutionary Dynamics of *Drosophila melanogaster* Populations Adapted for Larval Crowding**” submitted by Mr. Sayyed Imran Rashid (Reg. No. MS15139) for the partial fulfilment of BS-MS dual degree programme of the Institute, has been examined by the thesis committee duly appointed by the Institute. The committee finds the work done by the candidate satisfactory and recommends that the report be accepted.

Dr. Manjari Jain      Dr. Rhitoban Ray      Dr. N. G. Prasad      Prof. Sutirth Dey  
Choudhury                  (Supervisor)                  (Co-supervisor)

Dated: April 24, 2020



## **Declaration**

The work presented in this dissertation has been carried out by me under the guidance of Dr. N. G. Prasad at the Indian Institute of Science Education and Research Mohali and Prof. Sutirth Dey at the Indian Institute of Science Education and Research Pune.

This work has not been submitted in part or in full for a degree, a diploma, or a fellowship to any other university or institute. Whenever contributions of others are involved, every effort is made to indicate this clearly, with due acknowledgement of collaborative research and discussions. This thesis is a bonafide record of original work done by me and all sources listed within have been detailed in the bibliography.

Sayyed Imran Rashid

(MS15139)

Dated: April 24, 2020

In my capacity as the supervisor of the candidate's project work, I certify that the above statements by the candidate are true to the best of my knowledge.

Dr. N. G. Prasad

(Supervisor)

Prof. Sutirth Dey

(Co-supervisor)



# List of Figures

2.1	Ecological dynamics in a vial during larval feeding . . . . .	8
2.2	Flowchart of the larval stage in the model . . . . .	9
2.3	Waste build-up in the feeding band . . . . .	11
2.4	Change in the food quality of feeding band . . . . .	12
3.1	Effect of initial feeding rate and efficiency on body size . . . . .	16
3.2	Effect of initial feeding rate and efficiency on development time . . . .	17
3.3	Effect of initial feeding rate and efficiency on survivorship . . . . .	17
3.4	Effect of initial feeding rate and efficiency on final feeding rate . . . .	17
3.5	Effect of initial feeding rate and critical size on body size . . . . .	18
3.6	Effect of initial feeding rate and critical size on development time . .	19
3.7	Effect of initial feeding rate and critical size on survivorship . . . . .	19
3.8	Effect of initial feeding rate and critical size on final feeding rate . .	19
3.9	Effect of critical size and efficiency on body size . . . . .	20
3.10	Effect of critical size and efficiency on development time . . . . .	21
3.11	Effect of critical size and efficiency on survivorship . . . . .	21
3.12	Effect of critical size and efficiency on final feeding rate . . . . .	21
4.1	Model flowchart . . . . .	25
4.2	Timeseries for initial feeding rate . . . . .	26
4.3	Timeseries for efficiency . . . . .	27
4.4	Timeseries for critical size . . . . .	27
4.5	Timeseries for waste tolerance . . . . .	28
4.6	Mean body size of MB, MCU and CCU populations at 50 <sup>th</sup> generation in three different larval densities . . . . .	29

4.7	Mean survivorship of MB, MCU and CCU populations at 50 <sup>th</sup> generation in three different larval densities . . . . .	29
4.8	Mean time to reach critical size of MB, MCU and CCU populations at 50 <sup>th</sup> generation in three different larval densities . . . . .	30
5.1	Effect of initial variation in initial feeding rate and efficiency. . . . .	33
5.2	Effect of initial variation in initial feeding rate and critical size. . . . .	33
5.3	Effect of initial variation in critical size and efficiency. . . . .	34
5.4	Effect of heritability in initial feeding rate and efficiency on mean trait values at generation 50. . . . .	35
5.5	Effect of heritability in initial feeding rate and critical size on mean trait values at generation 50. . . . .	37
5.6	Effect of heritability in critical size and efficiency on mean trait values at generation 50. . . . .	38
6.1	Mean trait value distribution of MB, MCU, CCU and LCU populations in 60 eggs / 6 ml density at 50 <sup>th</sup> generation . . . . .	41
6.2	Mean trait value distribution of MB, MCU, CCU and LCU populations in 600 eggs / 1.5 ml density at 50 <sup>th</sup> generation (errorbars represent 95% CI) . . . . .	42
6.3	Mean trait value distribution of MB, MCU, CCU and LCU populations in 1200 eggs / 3 ml density at 50 <sup>th</sup> generation (errorbars represent 95% CI) . . . . .	43
6.4	Mean trait value distribution of MB, MCU, CCU and LCU populations in 1200 eggs / 6 ml density at 50 <sup>th</sup> generation (errorbars represent 95% CI) . . . . .	44
6.5	Mean initial feeding rate distribution of MB, MCU, CCU and LCU populations in (a) 60 eggs / 6 ml, (b) 600 eggs / 1.5 ml, (c) 1200 eggs / 3 ml and (d) 1200 eggs / 6 ml densities (errorbars represent 95% CI)	46
6.6	Mean efficiency distribution of MB, MCU, CCU and LCU populations in (a) 60 eggs / 6 ml, (b) 600 eggs / 1.5 ml, (c) 1200 eggs / 3 ml and (d) 1200 eggs / 6 ml densities (errorbars represent 95% CI) . . . . .	47

6.7	Mean feeding rate at critical size of MB, MCU, CCU and LCU populations in (a) 60 eggs / 6 ml, (b) 600 eggs / 1.5 ml, (c) 1200 eggs / 3 ml and (d) 1200 eggs / 6 ml densities (errorbars represent 95% CI) . . . . .	48
6.8	Mean efficiency distribution of MB, MCU, CCU and LCU populations in (a) 60 eggs / 6 ml, (b) 600 eggs / 1.5 ml, (c) 1200 eggs / 3 ml and (d) 1200 eggs / 6 ml densities (errorbars represent 95% CI) . . . . .	49



# List of Tables

1.1	Larval stage maintenance in MB, MCU, CCU and LCU populations . . . . .	4
A.1	Distributions and values of larval trait parameters used for initiating the model . . . . .	57
A.2	Values of scaling parameters used in the model . . . . .	57
A.3	Values of larval parameters used for initiating the model . . . . .	58



# Contents

<b>Certificate of Examination</b>	i
<b>Declaration</b>	ii
<b>List of Figures</b>	v
<b>List of Tables</b>	ix
<b>1 Introduction</b>	1
<b>2 Modelling Larval Stage in a Vial</b>	7
2.1 Ecology of a Culture Vial . . . . .	7
2.2 Larval Stage Model . . . . .	8
2.3 Simulations for Feeding Band Dynamics . . . . .	11
<b>3 Interplay between Larval Trait Parameters</b>	15
3.1 Initial Feeding Rate and Efficiency . . . . .	16
3.2 Initial Feeding Rate and Critical Size . . . . .	18
3.3 Critical Size and Efficiency . . . . .	20
<b>4 Modelling Evolution of Life-history Traits</b>	23
4.1 Modelling Adult Stage . . . . .	23
4.2 Effect of Laral Crowding on the Evolution of Larval Trait Parameters	26
4.3 Evolution of Other Life-history Traits . . . . .	28
<b>5 Effects of Variation on the Evolution of Larval Trait Parameters</b>	31
5.1 Variation in the Initial Distribution of Larval Trait Parameters . . . . .	31
5.2 Heritability of Trait Parameters . . . . .	34

<b>6</b>	<b>Introducing Correlations in Larval Trait Parameters</b>	<b>39</b>
6.1	Distribution of Laral Traits with Development Time . . . . .	39
6.2	Effects of Negative Correlation between Feeding Rate and Efficiency .	45
<b>7</b>	<b>Discussion</b>	<b>51</b>
	<b>References</b>	<b>53</b>
<b>A</b>	<b>Tables</b>	<b>57</b>
A.1	Larval Trait Parameters . . . . .	57
A.2	Scaling Parameters . . . . .	57
A.3	Other Larval Parameters . . . . .	58

# Chapter 1

## Introduction

The theory of density-dependent natural selection was verbally introduced by MacArthur (1962), MacArthur and Wilson (1967) to explore the evolution of phenotypes dependent on the population density. It is considered to be a critical link between ecological and evolutionary dynamics (Mueller, 1997). Over many years, this theory has been modified mathematically and studied experimentally to understand density effects on the evolution in great detail (Anderson & Arnold, 1983; Asmussen, 1983; Clarke, 1972; Mueller, 1997; Roughgarden, 1971; Santos, Borash, Joshi, Boulnutay, & Mueller, 1997). Early experimental studies have also shown that selection at extreme densities causes selection for higher competitive ability since there is competition for limited resources (Joshi, Prasad, & Shakarad, 2001). Such competitive ability of an organism is composite phenotype determined by various life-history traits. Through these early studies, it was clear that density is a significant factor in determining the life-history of organisms which are essential for competitive ability. Competition plays a vital role in determining not only evolutionary outcomes of species but also ecological outcomes which affect population dynamics and interactions with other species (Case, 2000; Dey, Bose, & Joshi, 2012). Thus, in order to grasp a better understanding of density-dependent selection, exploring the effect of competitive ability on ecological and evolutionary dynamics becomes essential (Prasad & Joshi, 2003).

Over the last four decades, various *Drosophila melanogaster* laboratory populations have been used to study the evolution of life-history traits due to density-dependent selection. One of the first experimental evolution studies used r and K populations

of *Drosophila melanogaster* (Mueller & Ayala, 1981) ) to investigate the *r*- and *K*-selection theory by MacArthur (1962), MacArthur and Wilson (1967). In these populations, *r*-selection lines were maintained at low-density, giving density-independent selection. In contrast, lines for *K*-selection were maintained at extreme densities such that selection was density-dependent. As predicted by early mathematical models, these studies showed that *r*-selected populations favoured traits responsible for higher population growth rate at low densities but lower growth rate at extreme density. Bakker (1962), Burnet, Sewell, and Bos (1977) suggested that larval feeding rate, which is measured as retraction rate of cephalopharyngeal sclerites of the larva, is a critical factor in larval competitive ability. Experimental studies on *r*- and *K*-selection showed that *K*-selected populations have higher competitive ability along with increased larval feeding rate (Joshi & Mueller, 1988). This lead to the conclusion that larval feeding rate is a good measure of competitive ability in *Drosophila* larvae. These populations could not predict classical density-dependent outcomes such as higher efficiency of food into biomass conversion (Mueller, 1990). Another problem with these populations was that *r* populations were maintained in discrete generation cycles while *K* populations were maintained in overlapping generations.

The successive experimental evolution studies were aimed at tackling questions raised in experimental studies mentioned above, by having a stage-specific density-dependent selection in a new set of *D. melanogaster* populations (described in Joshi and Mueller, 1993). In this long-term evolution study, a set of larval crowding (CU) population, another set of adult crowding (UC) population and one set of uncrowded (UU) *D. melanogaster* population were used. CU population adapted to larval crowding through a similar set of traits seen in K populations. CU population had higher competitive ability than UU population at high-density which leads to increased pre-adult survivorship and decreased pre-adult development time (D. J Borash & Ho, 2001; Joshi & Mueller, 1993; Santos et al., 1997). Such competitive ability in CU larvae was due to increased feeding rate and increased nitrogenous waste tolerance at the cost of poor efficiency to convert food into biomass (Daniel J. Borash, Gibbs, Joshi, & Mueller, 1998; Joshi & Mueller, 1996; Shiotsugu, Leroi, Yashiro, Rose, & Mueller, 1997). These results established a canonical view of density-dependent se-

lection in *Drosophila* which argued that the evolution of greater competitive ability occurred through increased feeding rate and metabolic waste tolerance at the cost of efficiency of food utilization (Joshi et al., 2001).

After the canonical view on adaptation to larval crowding was accepted widely, recent studies in different *Drosophila* species questioned this view. A subsequent study on adaptation to larval crowding involved *D. ananassae* and *D. nasuta nasuta* species of *Drosophila* which were wild-caught and subjected to long-term selection experiments similar to UU-CU populations (Nagarajan et al., 2016). Unlike CU population these were maintained at similar larval density but with decreased absolute number of eggs and total larval food. Due to adaptation to larval crowding in these populations, there was an increase in pre-adult survivorship at high-density and faster development compared to control at both low and high-density. In contrast to results from previous K and CU populations, these populations showed a reduction in time to reach critical size with no increase in larval feeding rate nor in nitrogenous waste tolerance (Nagarajan et al., 2016). Such reduced minimum critical feeding time was speculated to be due to increased efficiency of food into biomass conversion, which fit the *K*-selection theory of MacArthur and Wilson (1967). These surprising results were thought to be an outcome of several factors such as differences in species-specific genetic architect of traits responsible for larval competitive ability, differences in wild-caught populations and long-term laboratory populations, as well as differences in maintains of larval crowding suggesting the effect of ecological factors.

A long-term follow-up study on adaptation to larval crowding was performed using *Drosophila melanogaster* populations derived from UU populations to answer the questions raised from larval crowding studies of Nagarajan et al. (2016). In this study, a set of control populations (MB: Melanogaster Baseline) which had low larval density, and another set of populations (MCU: Melanogaster Crowded as larvae Uncrowded as adults) where larval stage was maintained at high-density similar to larval crowded populations of *D. ananassae* and *D. nasuta nasuta* (Sarangi, Nagarajan, Dey, Bose, & Joshi, 2016). MCU population showed the evolution of greater larval competitive ability through a similar set of traits observed in the study of Nagarajan et al.

(2016), i.e. decrease in the time to reach critical size without an increase in feeding rate. MCU larvae also did not differ in terms of metabolic waste tolerance but still showed faster pre-adult development time at both densities (Sarangi et al., 2016). In addition to these results, both MB and MCU populations showed a significant lower survivorship in the larval density of 1200 eggs / 6 ml food (CU-type culture) than in larval density of 600 eggs / 1.5 ml food (MCU-type culture) (Sarangi, 2013). MCU and CU population were derived from the same ancestry but still showed differences, indicating that ecological factors such as the overall number of eggs and total larval food, would be playing a significant role in determining which traits are selected for achieving greater competitive ability under larval crowding.

A subsequent study exploring ecological factors affecting adaptation to larval crowding involved two new set *D. melanogaster* populations derived from MB population. One set of these populations was CCU (Control Crowded as larvae Uncrowded as adults) population to address the effect of the absolute number of eggs and total food on evolution od larval competitive ability. Another set of populations was LCU (Larry Mueller Crowded as larvae Uncrowded as adults) population aimed at controlling for the food differences between CU and MCU populations since larval food used in these populations were banana and cornmeal medium respectively. In all these four *D. melanogaster* populations (MB, MCU, CCU and LCU) the adult stage was maintained in pretty much similar manner, whereas the details of larval stage maintenance are given in table 1.1 (Sarangi, 2018).

No.	Population	No. of eggs	Food volume	Vial dimensions
1.	MB	70	6 ml	9.5 cm h × 2.4 cm d
2.	MCU	600	1.5 ml	9.5 cm h × 2.4 cm d
3.	CCU	1200	3 ml	9.5 cm h × 2.4 cm d
4.	LCU	1200	6 ml	9.5 cm h × 2.2 cm d

Table 1.1: Larval stage maintenance in MB, MCU, CCU and LCU populations

After several generations of selection, CCU and LCU populations showed an increase in competitive ability and had higher pre-adult survivorship compared to MB population at high densities (Sarangi, 2018). These two populations showed much higher

feeding rate along with no difference in nitrogenous waste tolerance for achieving greater competitive ability, unlike MCU population. These results were interesting since MCU and CCU populations were maintained at the same larval density with varying total number of eggs and food. Sarangi (2018) also showed that feeding rate measured at the third instar stage of these larvae was dependent on the number of larvae present during larval feeding when assayed in slial (slide vials) treatment. When assayed inside culture vials, it was observed that the overall feeding rate of MCU population was the highest in all three high-density treatments in contrast to previous results performed on petri-dish. This result suggested that the ecological dynamics of the culture vial does play an essential role in determining competitive ability. Inside a culture vial, larval feeding occurs only at the topmost part of total food present due to their inability to dig more (Godoy-Herrera, 1977). This available upper part of the total food is approx 1 cm in the height of a standard vial used in MB, MCU and CCU populations, and is called as 'feeding band' (Sarangi, 2018). Thus, the sufficient larval density, i.e. number of larvae per feeding band is double in CCU population than in MCU population. Another significant finding regarding ecological dynamics inside a culture vial was the diffusion of metabolic waste excreted by larvae from the feeding band into the food below (Sarangi, 2018). In MCU culture vials, the total amount of food is almost similar to the size of the feeding band. This lead to the speculation that in MCU culture vial, there is little-to-no diffusion of metabolic waste from the feeding band and food quality may decrease very rapidly during larval feeding affecting competitive ability. In CCU and LCU culture vials, diffusion of such metabolic waste occurs from the feeding band which leads could lead to a slower decrease in food quality affecting competitive ability in a manner different than in MCU culture vial.

In MCU, CCU and LCU populations, apart from pre-adult survivorship and feeding rate, other life-history traits such as dry weight at eclosion, development time also evolved differently (Sarangi, 2018). Experimental studies are limiting in order to understand above-mentioned ecological factors inside culture vials of these populations. Thus, a computational simulation approach can be helpful to delve into ecological and evolutionary dynamics in these *Drosophila* populations.

In this thesis, I have presented a precursory stage-structured individual-based model to investigate adaptation to larval crowding in different crowding conditions based on the study of Sarangi (2018). This model is aimed at linking various ecological factors inside a culture vial, with the evolution of fitness-related traits and greater competitive ability through a combination of various larval traits. The later part of the model is also used to explore the role of initial standing variation in the population as well as heritability of larval traits, in determining the evolutionary trajectories to achieve greater competitive ability.

# **Chapter 2**

## **Modelling Larval Stage in a Vial**

Competition for food during the larval stage is determined by not only larval density but also ecological factors inside a food vial such as nitrogenous waste build-up, diffusion of waste in the food below, total food amount (Sarangi, 2018). Thus, in order to investigate the adaptation to larval crowding, it is crucial to understand the ecology of a vial in which the 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 behaviour in response to the various levels of larval crowding (Sarangi, 2018). Based on these experimental studies, I have created an individual-based model which considers larval trait parameters such as - feeding rate, efficiency to convert food into biomass, critical size and waste tolerance, to measure other traits like larval body size, development time, and survivorship.

### **2.1 Ecology of a Culture Vial**

During larval feeding inside a vial, larvae can 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, and this accessible part of the food is referred as the feeding band (Godoy-Herrera, 1977; Sarangi, 2018). For simplicity, feeding band is taken as volume of food proportional to the width 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 (In LCU culture vials, it is feeding band is smaller). In the model, the growth of larvae is affected by waste build-up and food quality in the feedin 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.

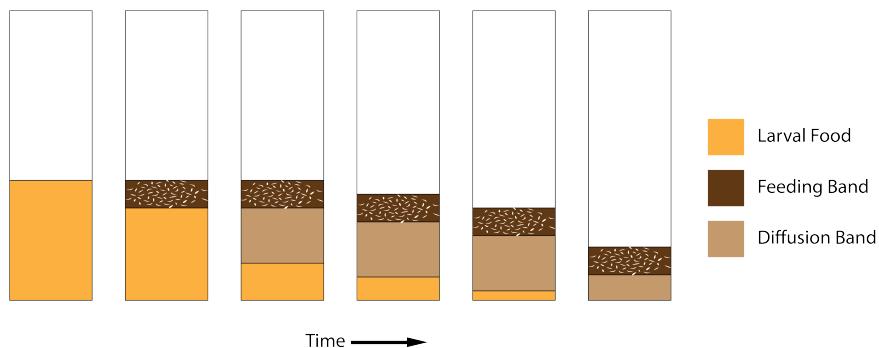


Figure 2.1: Ecological dynamics in a vial during larval feeding

## 2.2 Larval Stage Model

Each individual egg is assigned larval trait parameters from respective distributions with certain mean and variation given in table A.1. For a given amount of food and number of eggs, the model follows certain set of rules as described in fig 2.2 which are simulated in discrete time steps. The sex ratio within eggs is kept 1:1. 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 20% higher than that of males, so that females attain higher body size in the same time period as males but survivorship between sexes is same. (Joshi, Knight, & Mueller, 1996; Testa, Ghosh, & Shingleton, 2013)

The initial 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. 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  $t$

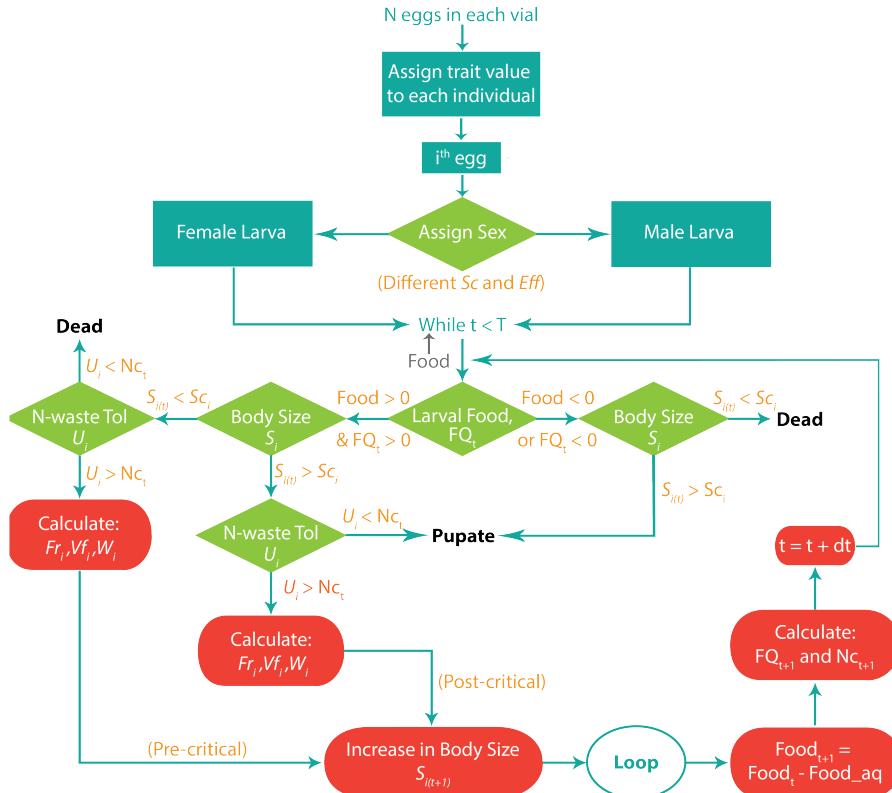


Figure 2.2: Flowchart of the larval stage in the model

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

$$\text{FoodEaten}(t) = \sum_i \text{food\_eaten}_i(t) = \sum_i Fr_i(t) \cdot V_f$$

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

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

Here,

$\epsilon_i$ : 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 all parameters used in the larval stage of the model, are given in table A.1, table A.2 and table A.3. These values were obtained by calibrating survivorship, body size and development time results similar to the empirical results in various larval densities Sarangi, 2018.

## 2.3 Simulations for Feeding Band Dynamics

Simulations are performed for trait values in table A.1 to observe the waste build up dynamics and food quality decrease in a food vial with different larval densities during larval feeding.

### 2.3.1 Waste build-up dynamics results

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.

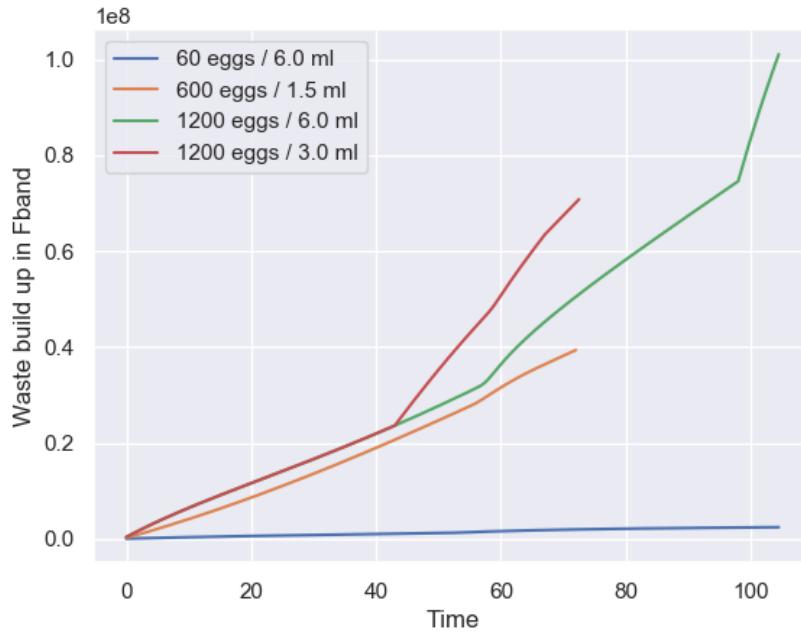


Figure 2.3: Waste build-up in the feeding band

High densities of 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. 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-up is almost in same quantity 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 availability 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 of waste build in the feeding band similar to CCU culture vial, but shows increase in the rate of waste build up approx. after  $60^{th}$  time step. This is due to the food is still available below the feeding band. 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.

### 2.3.2 Food quality dynamics results

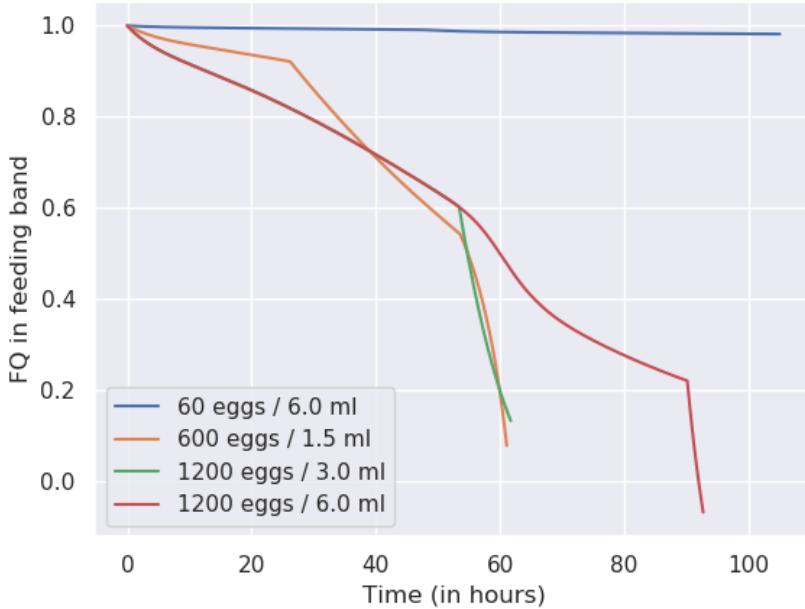


Figure 2.4: Change in the food quality of feeding band

Fig 2.4 shows the decrease in the quality of the food present in the feeding band. Food quality being negatively correlated with the amount of waste build-up in the feeding band, it shows patterns similar to waste build-up during larval growth in all crowding conditions. Since food quality affects body size increment at each time step. Body

size increment between  $40^{th}$  and  $60^{th}$  time step is completely different in MCU and CCU cultures even though there larval density is equal. In LCU culture, decrease in food quality is similar to CCU culture till  $60^{th}$  time step but later decreases gradually unlike CCU. This gradual decrease is due to gradual waste diffusion into the available food below the feeding and diffusion band. Once diffusion band hits the bottom at  $90^{th}$  time step, food quality decreases rapidly.



# Chapter 3

## Interplay between Larval Trait Parameters

In the larval stage model, 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 effects 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. Also, time to reach critical size is taken as a proxy for development time since time period between critical size and pupation is taken as a constant in all densities (ref). Larval stage is simulated to obtain body size, development time, final feeding rate (at critical size) and survivorship in MB, MCU and CCU cultures for each combination of initial feeding rate, efficiency and critical size from respective range of mean trait values. Here, effect of waste tolerance is ignored since no significant effect was observed on the body size, development time, final feeding rate and survivorship. Using experimental data and these simulation results, best combination of trait values are obtained which represents ancestral trait values for each population. Traits measured using these trait values represent MB flies from the experimental data and these trait values are used in further simulations.

### 3.1 Initial Feeding Rate and Efficiency

All simulation results show that the larval body size, development time, final feeding rate and survivorship are dependent on the larval density. In MCU and CCU culture, overall body size and survivorship are lesser while development time and final feeding rate are always higher for the same range of trait values than in MB culture (see fig 3.1 - fig 3.12). The larval body size is positively correlated with both initial feeding rate and efficiency at low density (MB culture), while at high densities (MCU and CCU cultures) it is positively correlated only with efficiency (see fig 3.1). In MCU culture, body size is not affected by the initial feeding rate unlike in CCU culture where initial feeding rate gives lesser body size. Fig 3.2 shows a negative correlation of development time i.e. time to reach critical size with both initial feeding rate and efficiency at all larval densities. survivorship is logically dependent on efficiency only in MCU and CCU cultures (see fig 3.3). In MCU culture, survivorship does not show any dependence on initial feeding rate, but in CCU culture it shows a slight negative correlation with initial feeding rate. At all larval densities, final feeding rate is positively correlated with initial feeding rate and negatively with efficiency (see fig 3.4). In MCU and CCU culture, final feeding rate show exponential dependence with efficiency which increases more with higher initial feeding rate.

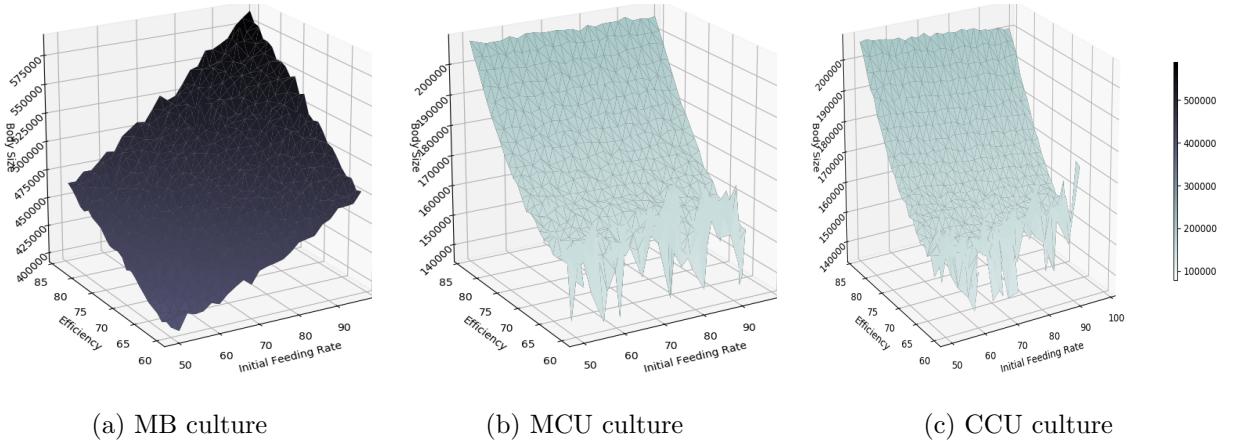


Figure 3.1: Effect of initial feeding rate and efficiency on body size

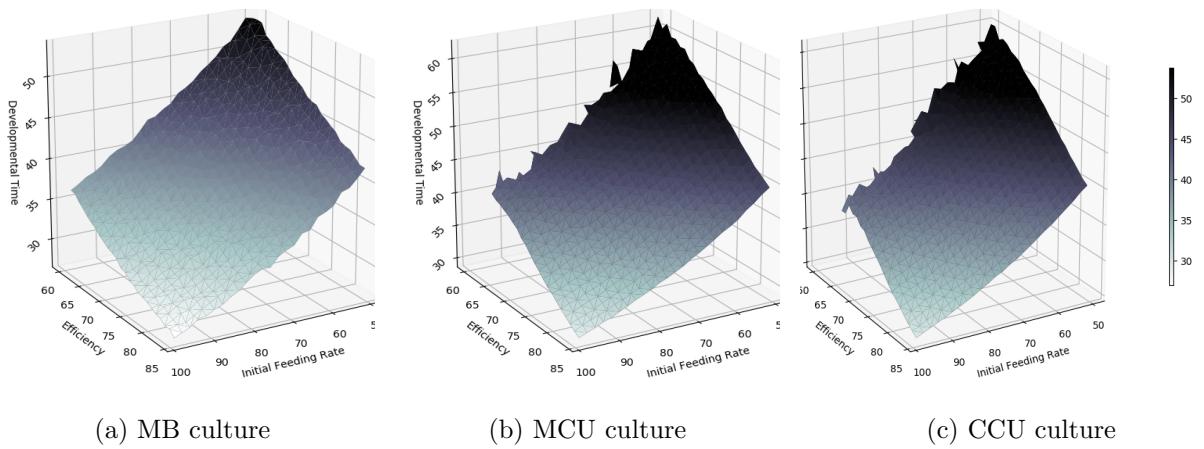


Figure 3.2: Effect of initial feeding rate and efficiency on development time

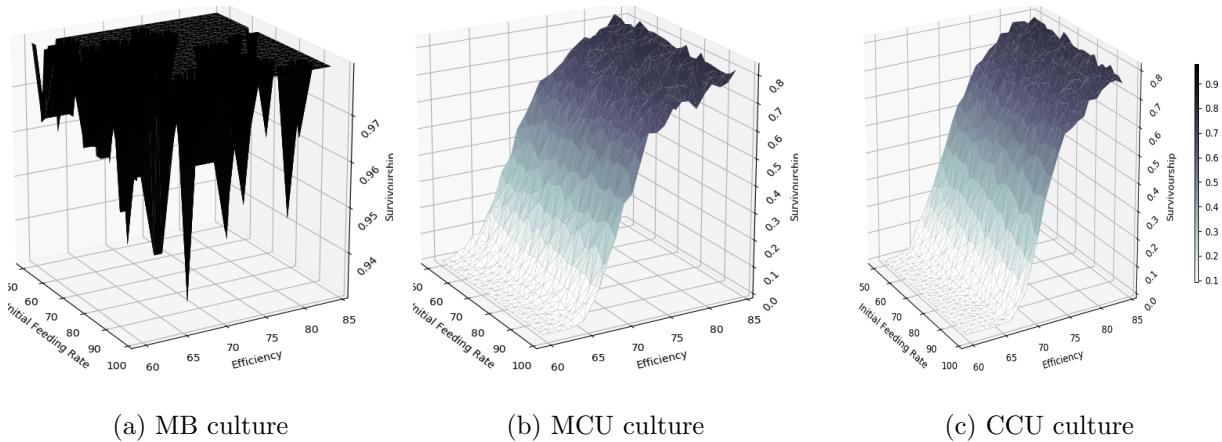


Figure 3.3: Effect of initial feeding rate and efficiency on survivorship

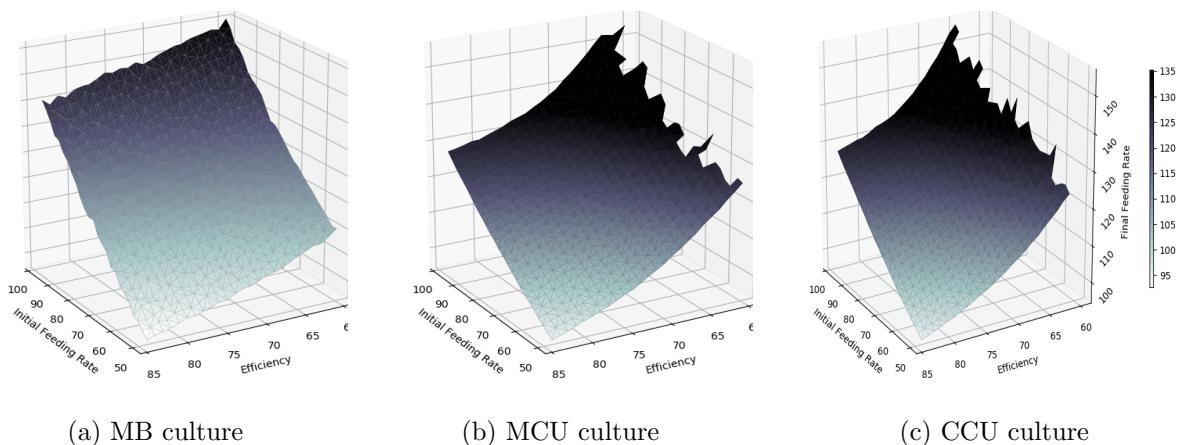


Figure 3.4: Effect of initial feeding rate and efficiency on final feeding rate

### 3.2 Initial Feeding Rate and Critical Size

For simulations varying parameter range of mean trait values of initial feeding rate and critical size, all traits show similar pattern with varying density as seen with previous simulations. The larval body size shows similar correlations with initial feeding rate and critical size in MB and MCU culture as seen in simulations varying initial feeding rate and efficiency (see fig 3.5). In CCU culture, body size is negatively correlated with initial feeding rate only for smaller values of critical size, but it is not affected by initial feeding rate at larger critical size values. Fig 3.6 shows a negative correlation of development time with initial feeding rate, but positive correlation with critical size in all culture vials. Survivorship is logically dependent on critical size only in MCU and CCU culture. In MCU and CCU cultures, survivorship shows a slight negative correlation with initial feeding rate (see fig 3.7). At all larval densities, final feeding rate is positively correlated with both initial feeding rate and critical size (see fig 3.8).

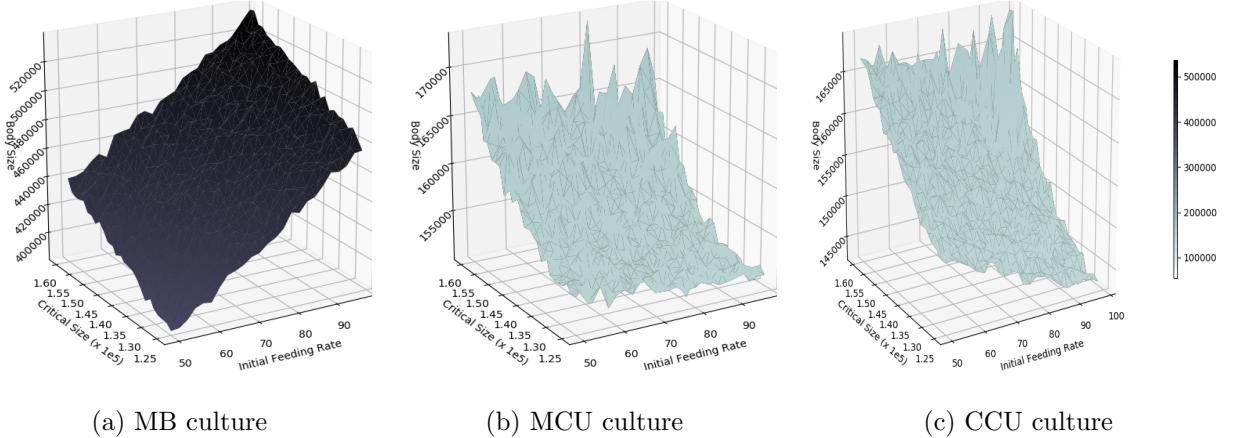


Figure 3.5: Effect of initial feeding rate and critical size on body size

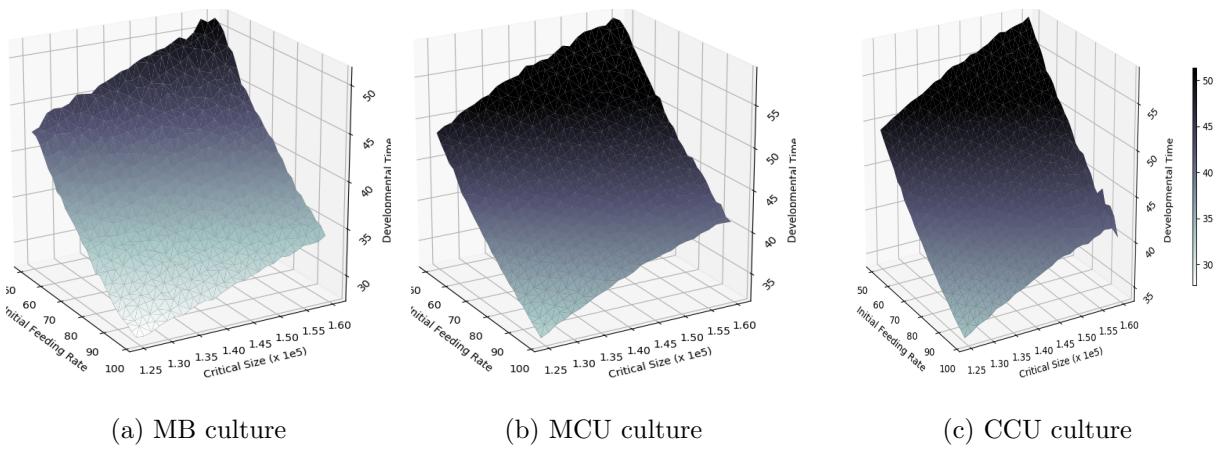


Figure 3.6: Effect of initial feeding rate and critical size on development time

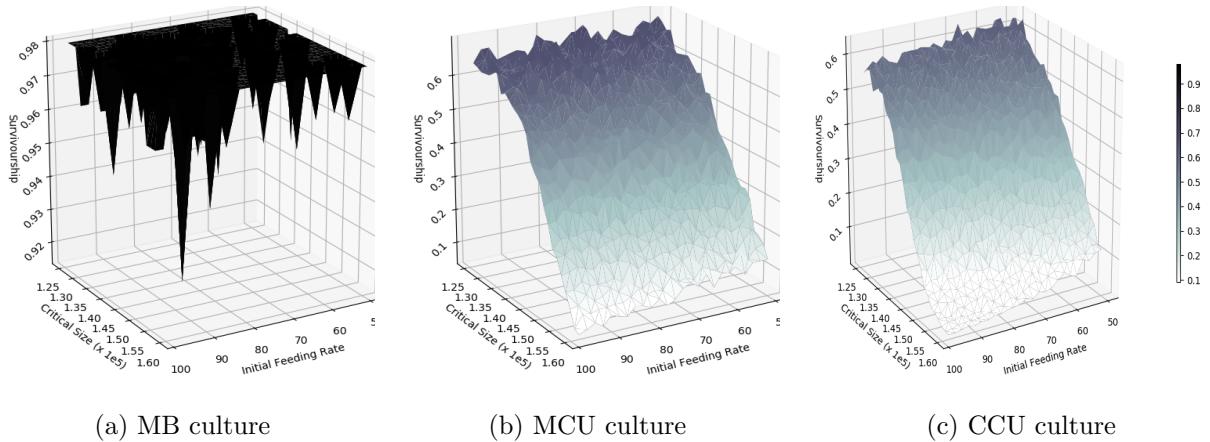


Figure 3.7: Effect of initial feeding rate and critical size on survivorship

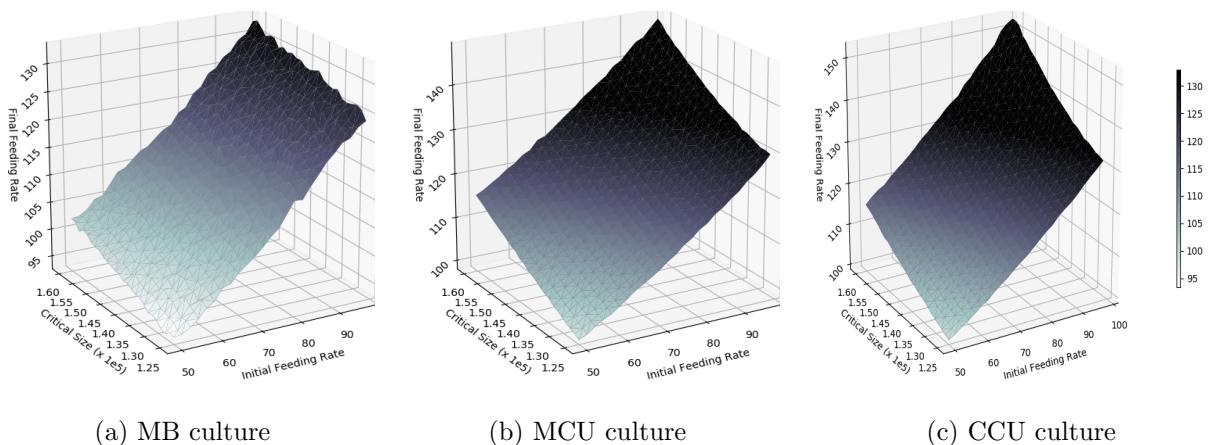


Figure 3.8: Effect of initial feeding rate and critical size on final feeding rate

### 3.3 Critical Size and Efficiency

In simulations varying parameter range of mean trait values of initial feeding rate and critical size, all traits measured show similar pattern with varying density as seen with previous simulations. The larval body size shows similar correlations with critical size and efficiency in MB culture as seen in simulations varying initial feeding rate and efficiency (see fig 3.9). In MCU and CCU cultures, body size is positively correlated with critical size only for smaller values of efficiency, but is not affected by critical size at larger efficiency values. Fig 3.10 shows a negative correlation of development time with efficiency, but positive correlation with critical size at all densities. survivorship is logically dependent on efficiency only in MCU and CCU culture. In MCU and CCU cultures, survivorship also shows a negative correlation with critical size at lower values of efficiency (see fig 3.11). At all larval densities, final feeding rate is positively correlated with critical size and negatively with efficiency (see fig 3.8).

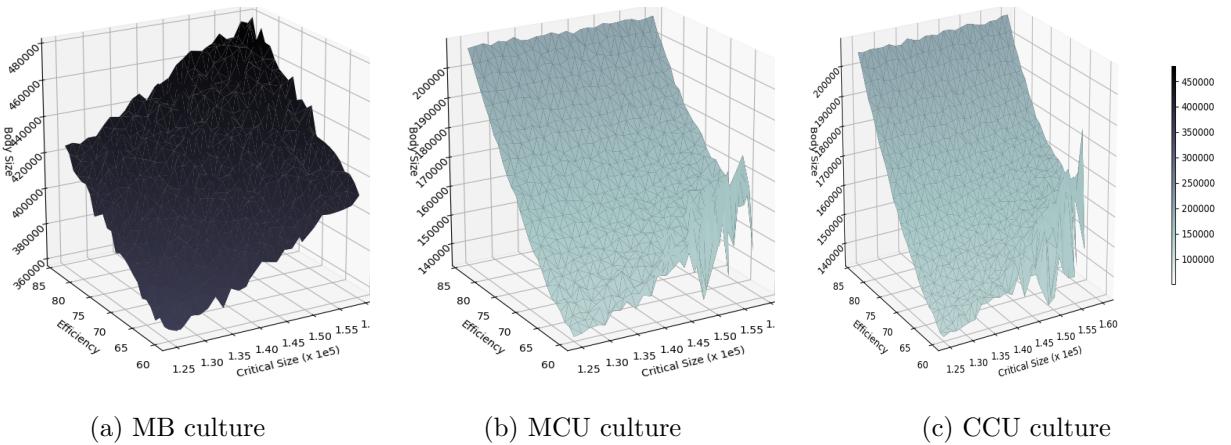


Figure 3.9: Effect of critical size and efficiency on body size

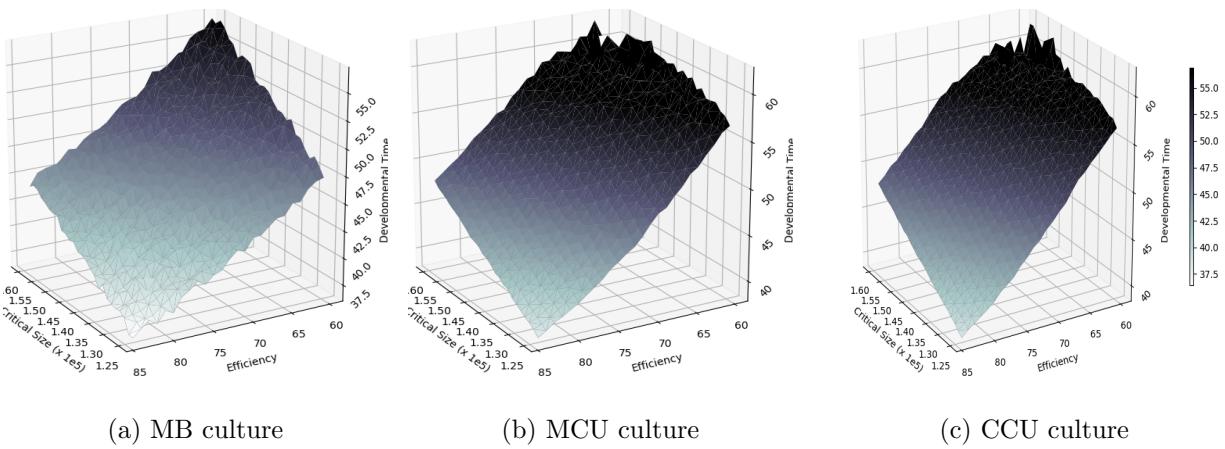


Figure 3.10: Effect of critical size and efficiency on development time

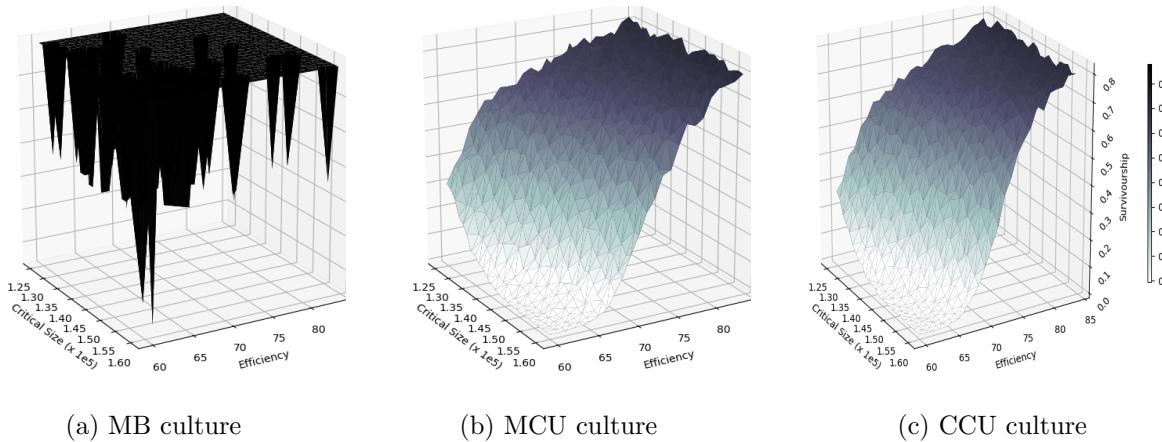


Figure 3.11: Effect of critical size and efficiency on survivorship

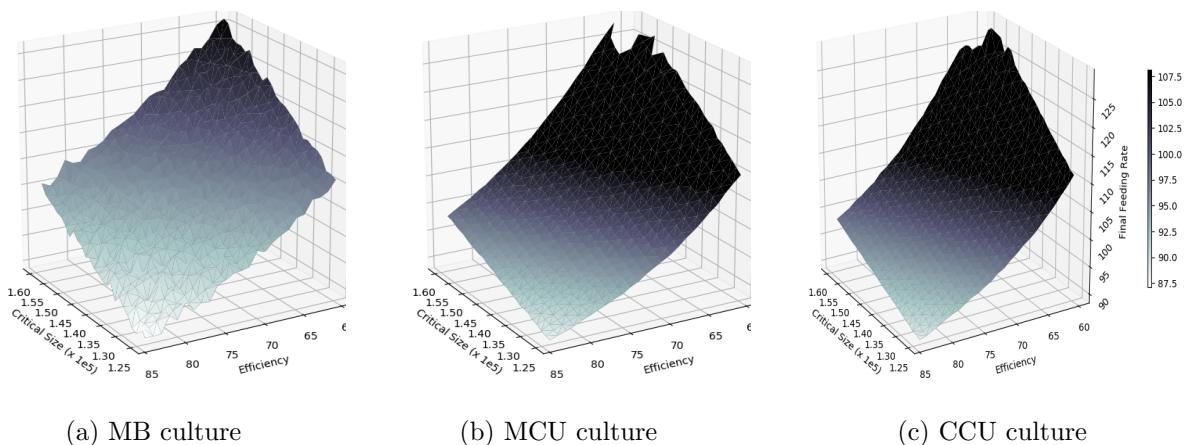


Figure 3.12: Effect of critical size and efficiency on final feeding rate



# 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 pupal and adult stage of *Drosophila* life cycle. After larval stage, surviving individuals go through pupal stage where some of them undergo pupal mortality. The adult stage includes randomly choosing surviving adults from all replicate vials of pupal stage, matings, and inheritance of larval trait parameters from parents to offspring. Female is mated once with random male chosen from the adult population ( $n = 2400$ ) with replacement for simplicity. From all the offspring produced, eggs are chosen at random for the next generation with numbers respective to the crowding environment maintained.

#### 4.1.1 Pupal stage

After collecting all the surviving individuals from the larval stage, a probability of death during pupal stage is assigned to each survived larva. This probability is dependent on the amount of waste accumulated in the body while econsuming food during the larval stage. This probability is given as:

$$P_M(i) = 1 - \exp(-(W_{acum}(i) \cdot x_3)^2)$$

Here,

$P_M$ : Probability of dying during pupal stage;

$W_{acum}(i)$ : Waste accumulated by  $i^{th}$  larva during larval stage;

$x_3$ : Scaling parameter.

#### 4.1.2 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:

$$Egg_i = Nut \cdot x_4 \cdot \log(x_5 \cdot s_i)$$

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;

$x_4, x_5$ : scaling parameters.

#### 4.1.3 Inheritance

Larval trait parameters (initial feeding rate, efficiency, 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 all offspring is calculated. This mid-parent value is taken as a mean of a normal distribution with fixed standard deviation for respective trait parameters. The standard deviation in this normal distribution determines the heritability 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 the trait  $T$  for a given mating;

$\delta_T$ : heritability of mid-parent value of the trait  $T$ ;

$N(mpv, \delta)$ : Normal distribution with  $mpv$  as mean and  $\delta$  as standard deviation.

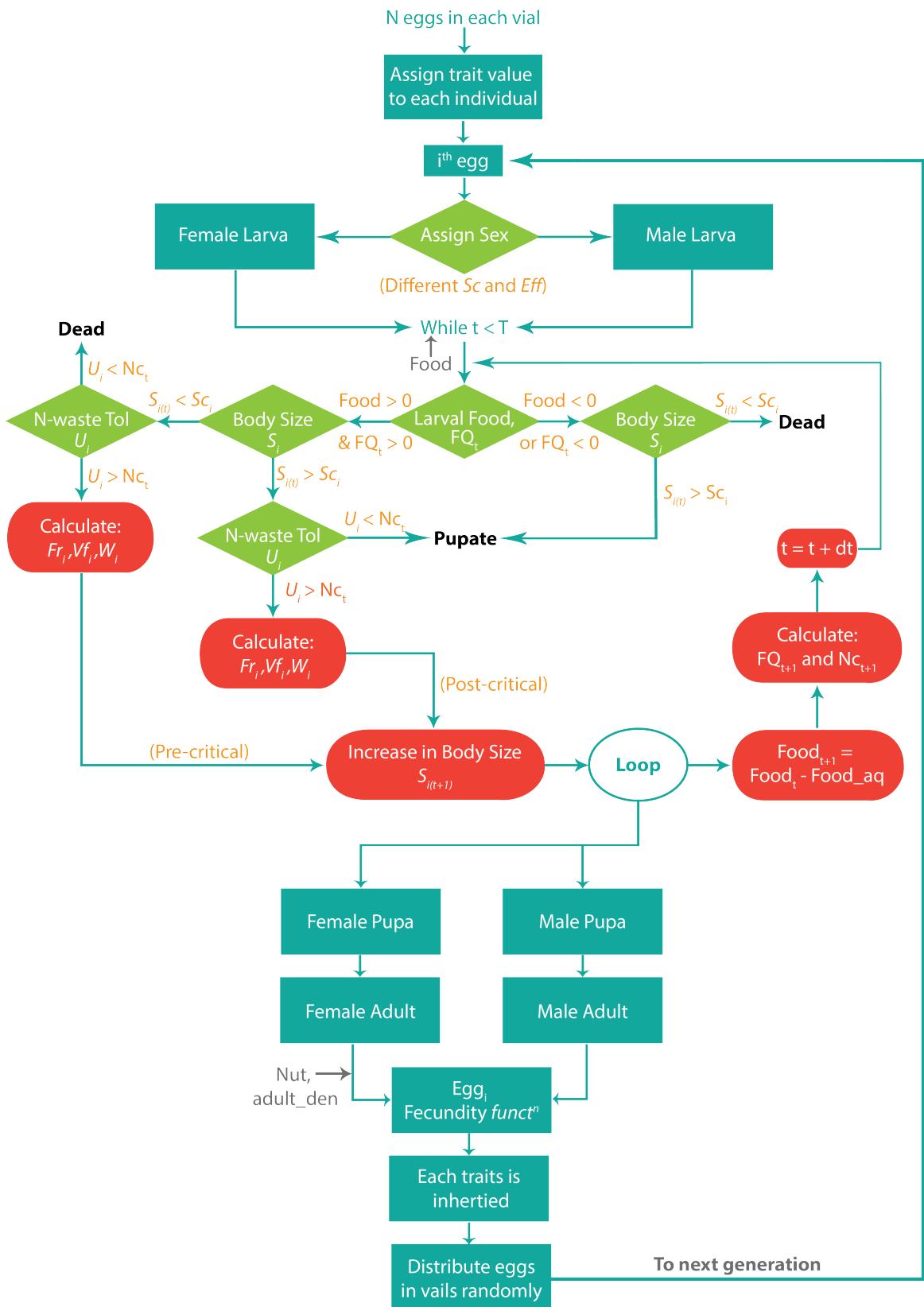


Figure 4.1: Model flowchart

## 4.2 Effect of Laral Crowding on the Evolution of Larval Trait Parameters

Using values for all parameters given in table A.3 and table A.2, the entire model is simulated for 100 generations with 10 replicates for MB, MCU and CCU cultures. The overall model follows the path shown in fig 4.1. All larval trait parameters are taken from independent distribution and there is no correlation between them (see table A.1). To see how larval trait parameters evolve over time, timeseries for these traits of surviving adult individuals are plotted with 95% CI.

In MB culture, being control population, none of the parameters evolve over time (see fig 4.2, fig 4.3, fig 4.4, fig 4.5). Initial feeding rate in high density cultures increase over generations at similar rate but initial feeding rate is higher always in CCU culture always than in MCU culture. 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. Critical size in high density cultures decreases at the same rate but critical size in CCU culture is always lower than in MCU culture. Waste tolerance does not evolve in all of the culture populations since there is no significant change in waste tolerance value.

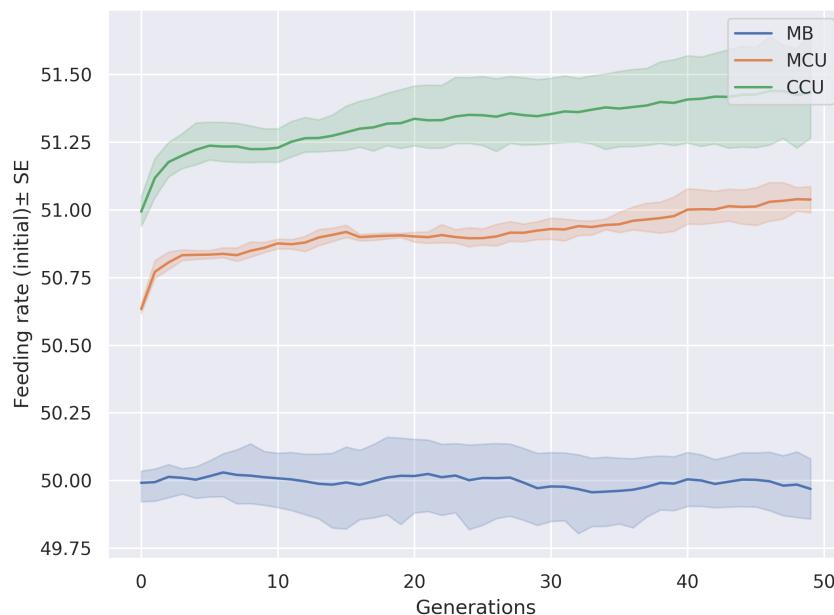


Figure 4.2: Timeseries for initial feeding rate

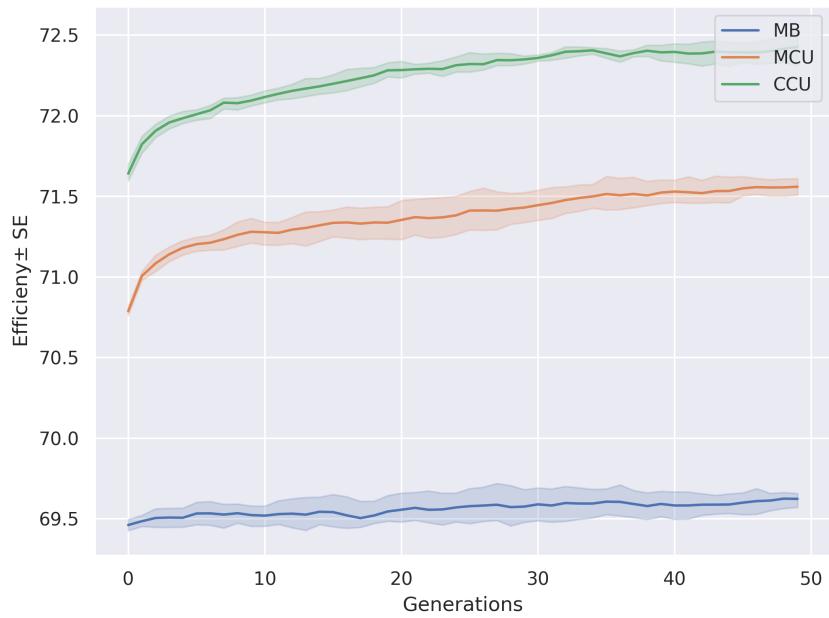


Figure 4.3: Timeseries for efficiency

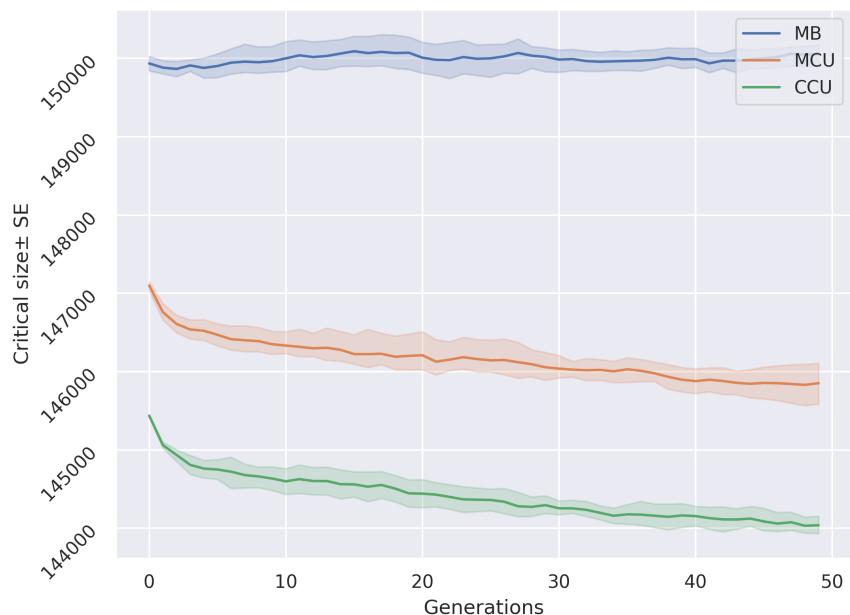


Figure 4.4: Timeseries for critical size

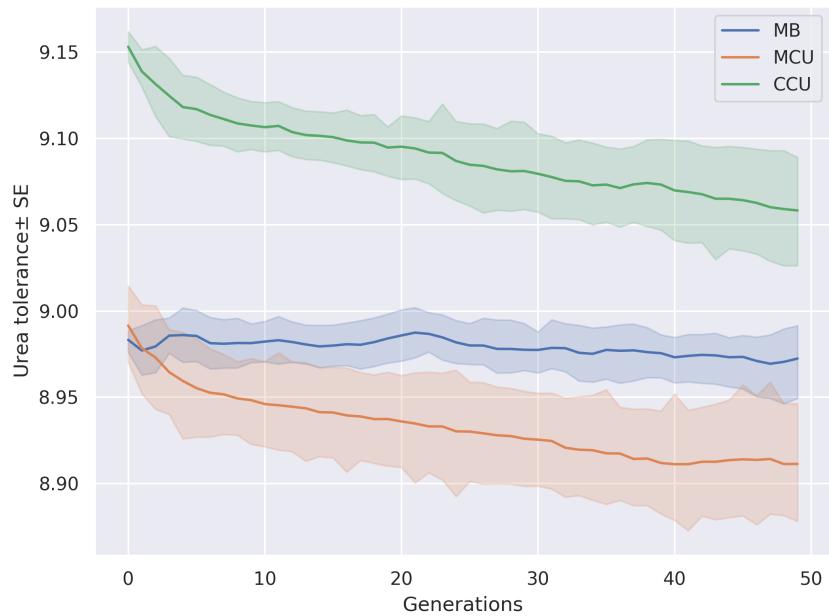


Figure 4.5: Timeseries for waste tolerance

### 4.3 Evolution of Other Life-history Traits

wee.

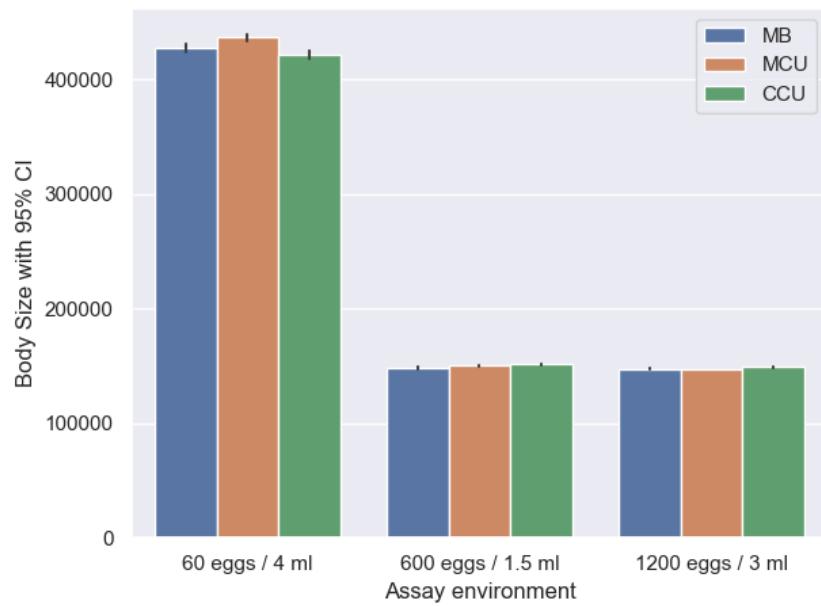


Figure 4.6: Mean body size of MB, MCU and CCU populations at 50<sup>th</sup> generation in three different larval densities

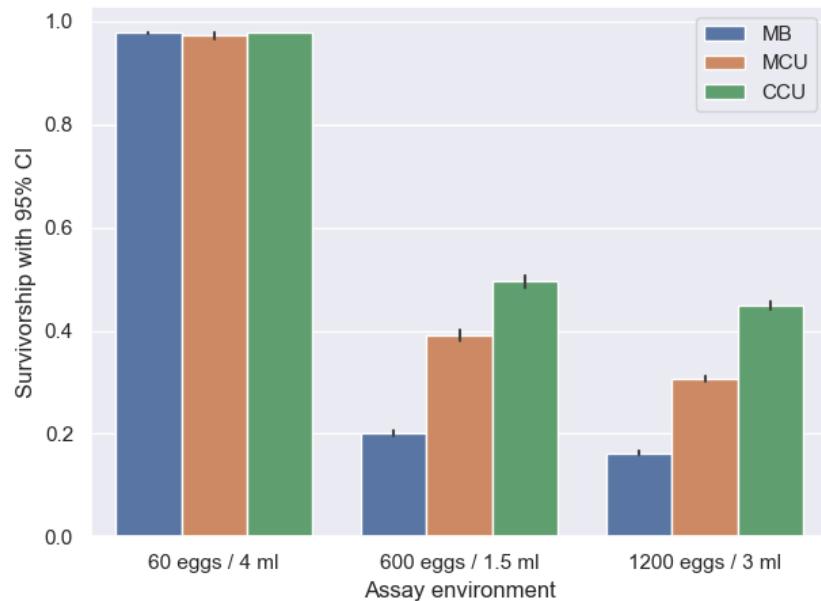


Figure 4.7: Mean survivorship of MB, MCU and CCU populations at 50<sup>th</sup> generation in three different larval densities

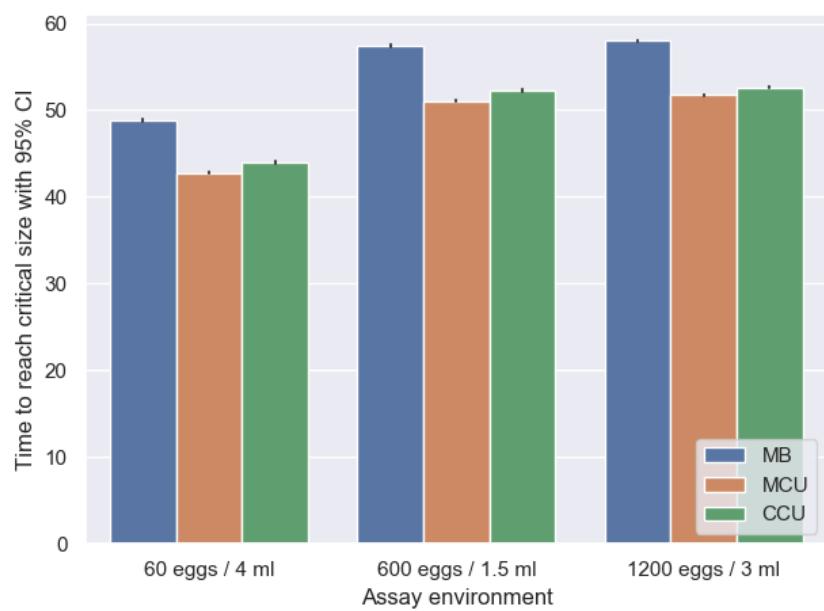


Figure 4.8: Mean time to reach critical size of MB, MCU and CCU populations at 50<sup>th</sup> generation in three different larval densities

# Chapter 5

## Effects of Variation on the Evolution of Larval Trait Parameters

The stochasticity in the model comes from the initial standing variation in the larval trait parameters as well as from the heritability of each trait parameter during the inheritance of those traits. The results from simulations show how these sources of variations play an important role in determining the evolutionary routes taken to increase fitness and achieve greater competitive ability.

### 5.1 Variation in the Initial Distribution of Larval Trait Parameters

In the initial distribution of each trait value, the variation comes from the standard deviation given for each distribution of the traits like feeding rate, waste tolerance, critical size and efficiency. The initial standing variation in these trait distributions determine the maximum mean trait value that can be achieved to increase the fitness. Simulations were performed for given fixed mean trait values but varying their respective initial standing variation to see how these variations interact to obtain maximum fitness in multiple ways at 50<sup>th</sup> generation. In fig 5.1 - 5.3, differences of the mean trait values of the population at 50<sup>th</sup> generation and 0<sup>th</sup> generation are plotted for

different combinations of initial variation in trait values. The initial standard deviation for a trait is taken as a certain percentage of its respective mean trait value at  $0^{th}$  generation. These initial conditions used in simulations are given in table (no.).

These results show that it is clear that differences in variation of these trait parameters give different mean trait values at  $50^{th}$  generation across different crowding densities. Overall there is no significant effect of initial variation in trait parameters on the mean trait values in MB culture is found. Higher initial variation in initial feeding rate and efficiency give higher mean initial feeding rate and mean efficiency respectively after  $50^{th}$  generation in MCU and CCU cultures without interacting with each other (see fig 5.1). There is no difference in mean trait values (initial feeding rate and efficiency) of MCU and CCU cultures. Initial feeding rate in MCU culture is lesser than in CCU culture only when initial variation is high and there is no interaction with variation in critical size at all densities (see fig 5.2). There is no significant effect on the mean critical size at  $50^{th}$  generation due to initial variation initial feeding rate and critical size at all densities. In Fig 5.3, initial variation in efficiency and critical size both interact with each other which give significant difference in mean efficiency in MCU and CCU cultures. At low initial variation of efficiency, there is no effect of initial variation in critical size on the mean efficiency which is same across MCU and CCU cultures (see fig 5.3). At high initial variation in efficiency and higher initial variation in critical size lead to difference in mean efficiency across MCU and CCU culture. At higher initial variation in efficiency but lower variation in critical size, there is no significant difference across MCU and CCU culture. Fig 5.3 shows the interaction of initial variation in efficiency and critical size in achieving higher efficiency across MCU and CCU cultures. There is no effect of these variations on mean critical size. There was no effect of these variations on waste tolerance and the graphs are given in appendix A2 (fig.A2).

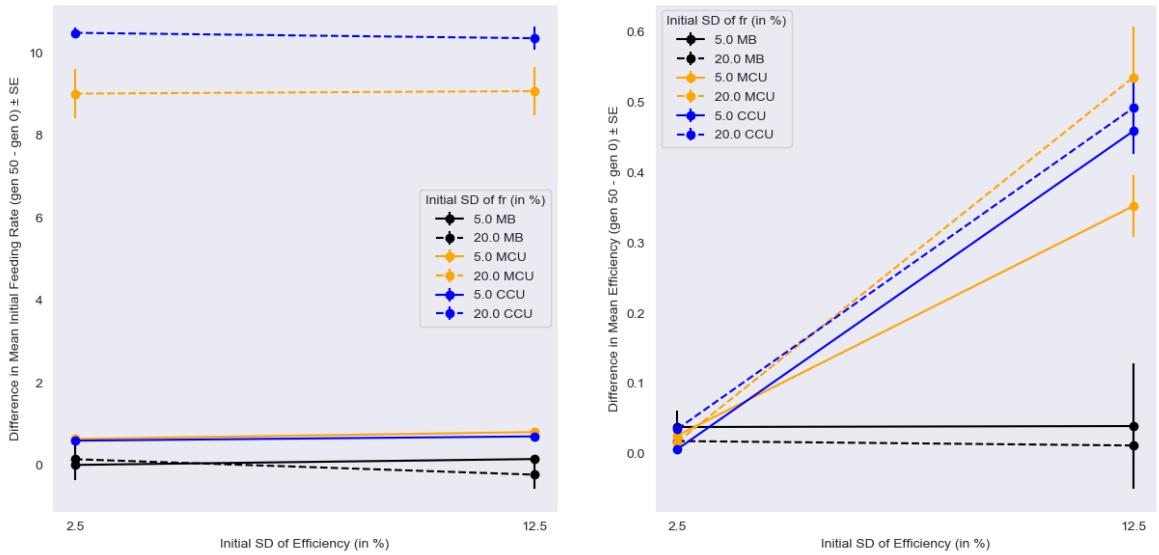


Figure 5.1: Effect of initial variation in initial feeding rate and efficiency.

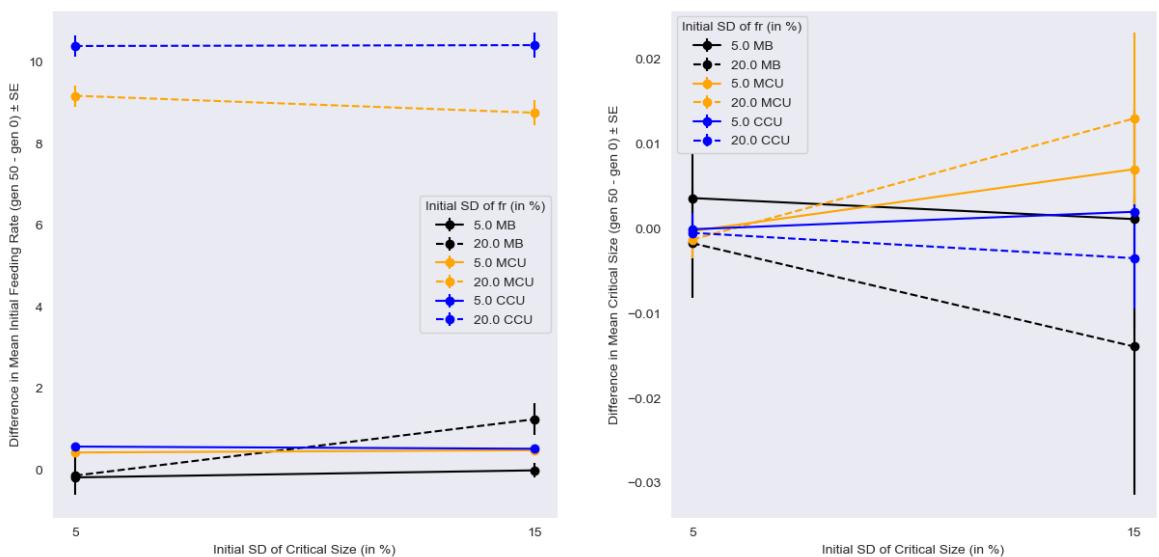


Figure 5.2: Effect of initial variation in initial feeding rate and critical size.

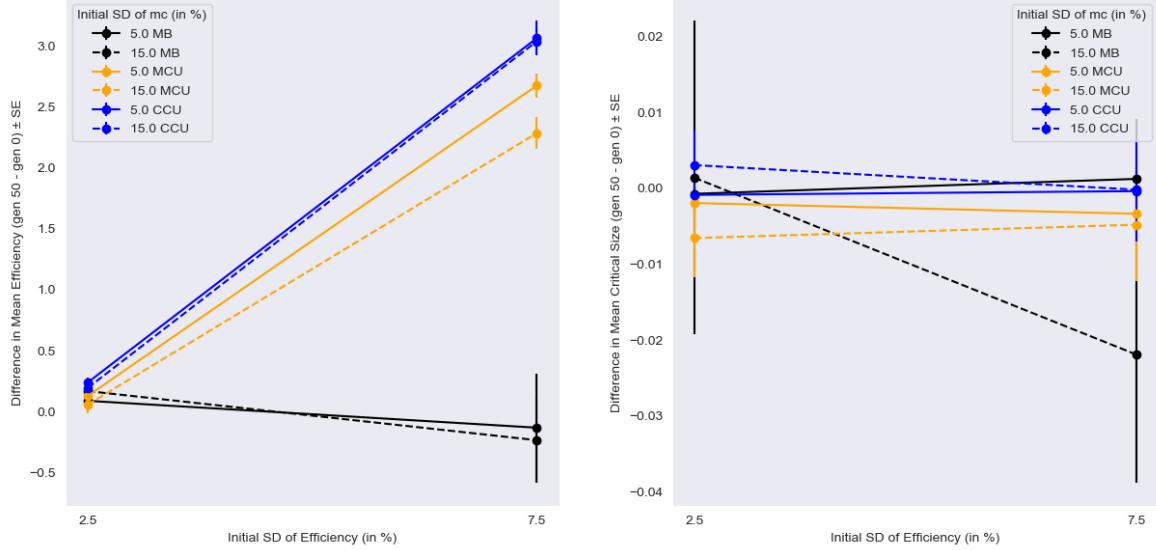


Figure 5.3: Effect of initial variation in critical size and efficiency.

## 5.2 Heritability of Trait Parameters

During the inheritance of trait parameters from parents to offspring, the variation in the trait value of offspring from the parents comes from heritability of that trait parameter. In the model, while assigning the trait value to the offspring from a normal distribution around mid-parent value as mean, the standard deviation ( $\omega$ ) of this distribution is taken as a measure of heritability. This standard deviation,  $\omega$ , is taken as a certain percentage of mean value of respective parameter at  $0^{th}$  generation. Higher the standard deviation, lesser is heritability for that trait parameter. For fixed initial conditions, simulations are performed with varying  $\omega$  for combinations of trait parameters across MB, MCU and CCU cultures (see table (no.)). The results from these simulations are plotted similar to initial variation plots (see fig 5.4 - 5.6).

Results from these simulations show that, initial feeding rate, efficiency and critical size do not show any significant effect of heritability of these trait parameters in MB culture. Higher heritability of initial feeding rate leads to higher mean initial feeding rate in both MCU and CCU culture. This mean feeding rate decreases with decrease in heritability of efficiency in MCU and CCU cultures only when heritability of feeding rate is high, otherwise the interaction with heritability of efficiency is only in CCU culture (fig 5.4). The only significant difference in mean efficiency is between

MCU and CCU culture when heritability of efficiency is less. There is no change in mean critical size due to heritability of these two trait parameters at all densities. Lesser heritability of efficiency also seems to cause increase in mean waste tolerance without any interaction with heritability of feeding rate in all cultures.

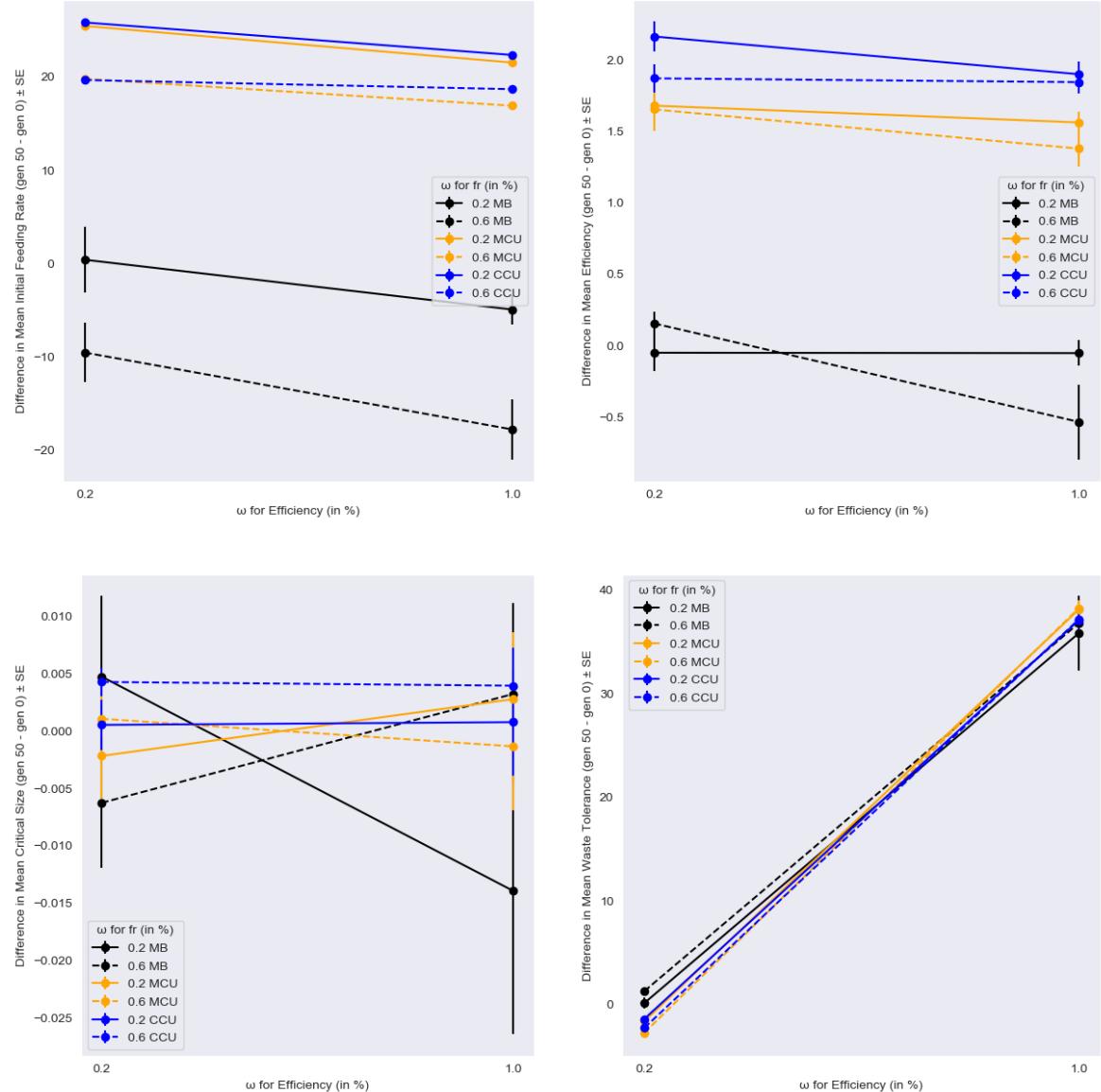


Figure 5.4: Effect of heritability in initial feeding rate and efficiency on mean trait values at generation 50.

Fig 5.5 shows that lesser heritability of critical size slightly affect lesser mean initial feeding rate when heritability of initial feeding rate is high in MCU and CCU cultures, but it this effect is only seen in CCU culture when heritability of initial feeding rate is low (fig 5.5). In MCU culture, mean efficiency is higher for higher heritability of initial feeding rate when heritability of critical size is high while there is no effect when heritability of critical size less. In CCU culture, here is no effect of heritability of initial feeding rate on mean efficiency when heritability of critical size is high, but it affects mean efficiency when heritability of critical size is less. The difference in mean efficiency between MCU and CCU cultures is present in all cases at higher heritability of critical size but it disappears when higher heritability of initial feeding rate is taken with lesse heritability of critical size. In MCU and CCU cultures, higher heritability of critical size leads to no decrease in mean critical size over generations. Lesser heritability of critical size causes decrease in critical size in MCU and CCU culures equally. This decrease is dependent on heritability of initial feeding rate, as higher heritability of it gives more decrease in mean critical size in both MCU and CCU cultures. There is no effect of the heritability of these trait parameters on mean waste tolerance.

Fig 5.6 shows no significant effect of heritability of critical size on mean initial feeding rate. At higher heritability of efficiency, mean initial feeding rate shows the difference between MCU and CCU culture. This difference between MCU and CCU cultures disappears when heritability of efficiency is less. Mean efficiency is higher for lesser heritability of efficiency and higher heritability of critical size, while in the vice versa case, there is no effect of heritability of critical size. The opposite scenario is seen for mean efficiency in CCU culture. The difference in mean efficiency between MCU and CCU culture is only seen when heritability of efficiency is high and of critical size is low. There is no effect of heritability of efficiency on mean critical size. Heritability of critical size only affects mean critIcal size when heritability of efficiency is high. Mean waste tolerance has a pattern similar to fig 5.4, showing that it is dependent on heritability of efficiency.

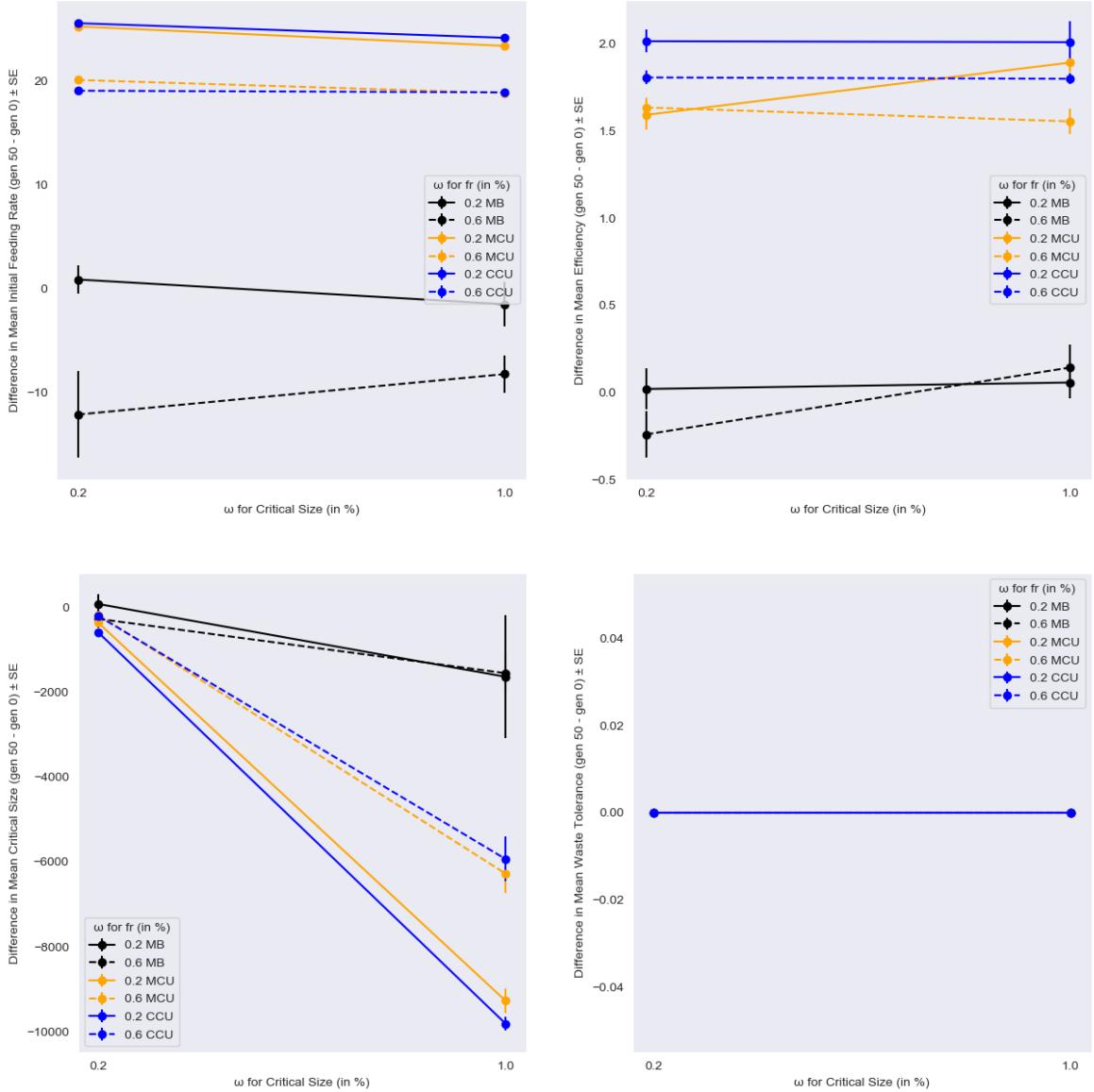


Figure 5.5: Effect of heritability in initial feeding rate and critical size on mean trait values at generation 50.

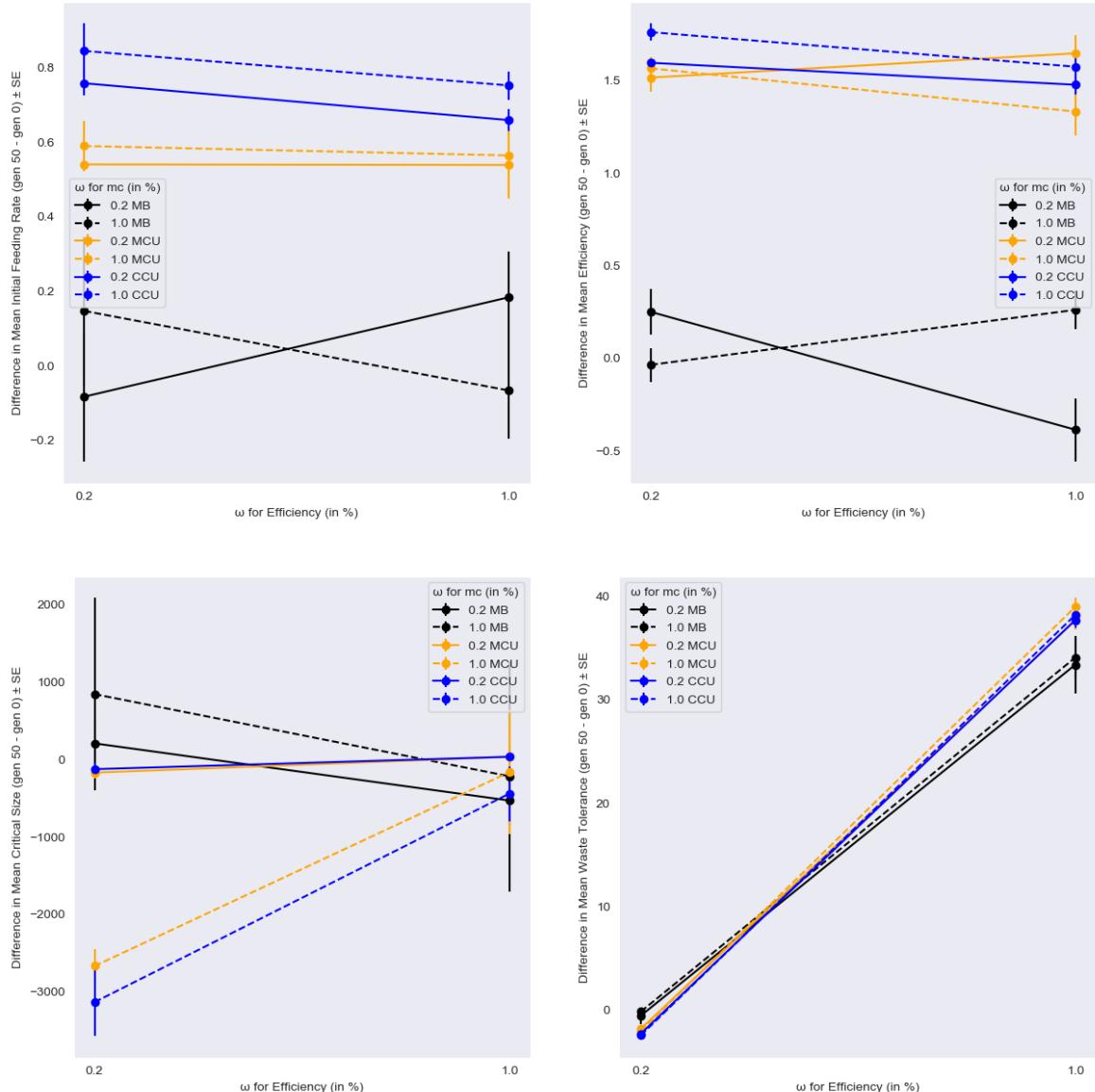


Figure 5.6: Effect of heritability in critical size and efficiency on mean trait values at generation 50.

# Chapter 6

## Introducing Correlations in Larval Trait Parameters

Larval trait parameters used in the model are considered to be independent of each other while assigning to each individual. This model can be useful to understand distributions of these trait parameters and other life-history traits with development time after few generations of selection in each density regime. It can also give more detailed insight on how larval trait parameters interact with larval density as well as how early eclosing and late eclosing flies are different in these populations.

### 6.1 Distribution of Laral Traits with Development Time

Simulations are run using the initial conditions for MB, MCU, CCU and MCU populations given in tabel (no.) at all four densities (replicates = 10, generation = 50). Results from these simulations are plotted for larval body size, final feeding rate (at critical size), efficiency, initial feeding rate, critical size and efficiency. Similar to previous simulations, time to reach critical size is taken as a proxy for development time (see fig 6.1 - 6.4). For each of the above traits, a scatter plot is plotted, where trait value is plotted as an 'x-estimator' of respective development time (ref). These plots give a clear visualization of mean trait value distribution with development time. Mean trait values towards the right side of the x-axis represent late eclosing flies where as such values towards left side of x-axis represent early eclosing flies.

In these plots, MB larvae take more to reach critical size compared to MCU, CCU and LCU larvae due to higher critical size, lesser efficiency and initial feeding rate. In MB culture (60 eggs / 6 ml), There is no pattern of body size, efficiency, initial feeding rate and waste tolerance with development time. Since critical size is higher for larvae with higher development time, final feeding rate is also higher in them across all populations (see fig 6.1).

In MCU culture (600 eggs / 1.5 ml), results are similar to mean trait value distributions in MB culture except, deacrese in mean body size of late eclosing ones in MCU population. Variation in mean body size is higher for both early and late developing larvae for all populations in this culture (see fig 6.2).

In CCU culture (1200 eggs / 3 ml), mean body size and efficiency stays constant across development time but the variation is very less for late developing larvae. Initial feeding rate is slightly higher with reduced variation for larvae with higher development time. Waste tolerance is higher with a decrease in variraiotn for late developing larvae (see fig 6.3).

In LCU culture (1200 eggs / 6 ml), mean trait values are similar to those in CCU culture except, mean body size, which shows that late developing larvae have similar body size as early ones. This forms a U-shapd mean trait value distribution. For late developing larvae in this culture, initial feeding rate is also lesser and variation in efficiency is higher across all popularions. Mean waste tolerance distribution show late developing larave have higher waste tolerance which is more prominent in MCU and LCU populations (see fig 6.4).

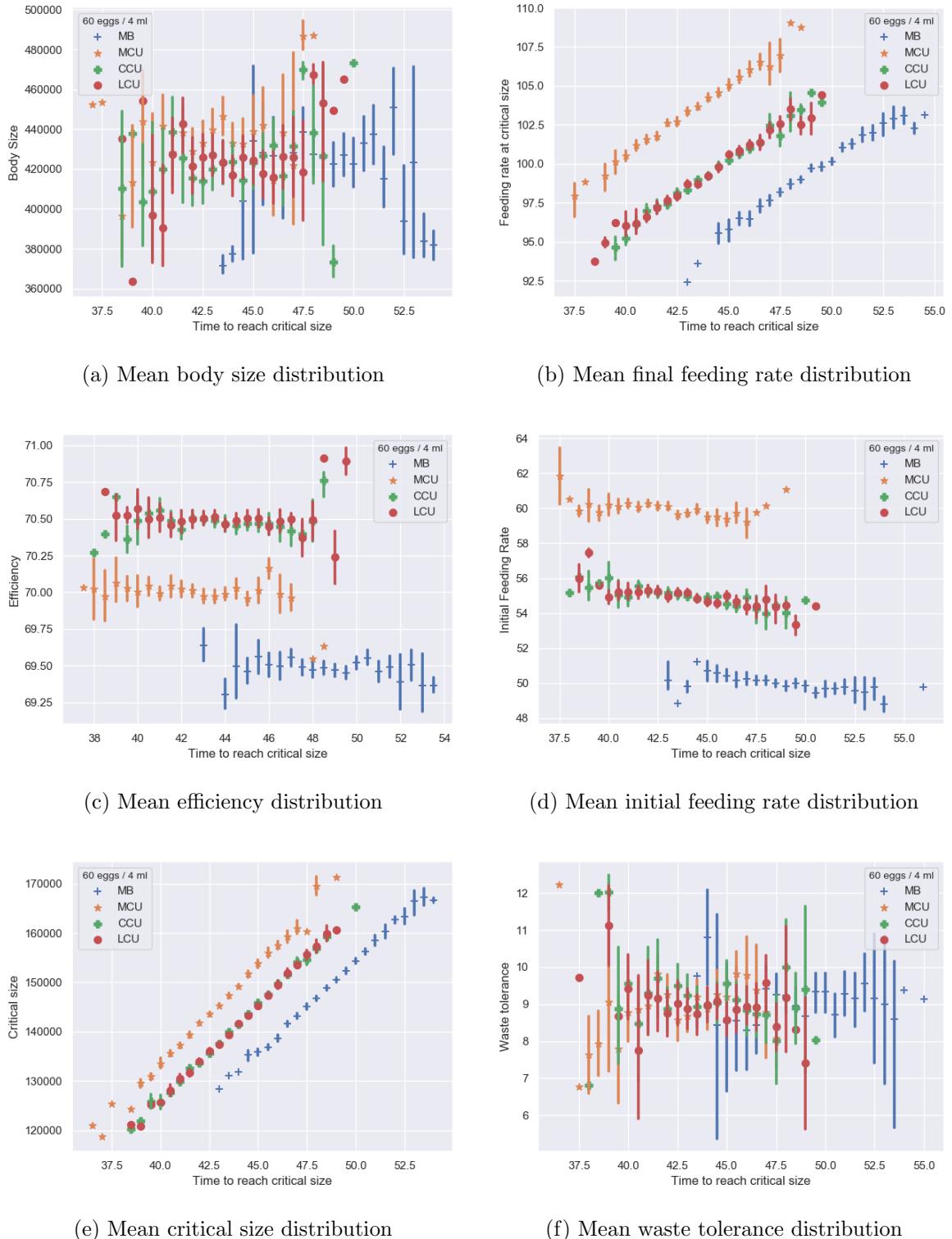


Figure 6.1: Mean trait value distribution of MB, MCU, CCU and LCU populations in 60 eggs / 6 ml density at 50<sup>th</sup> generation

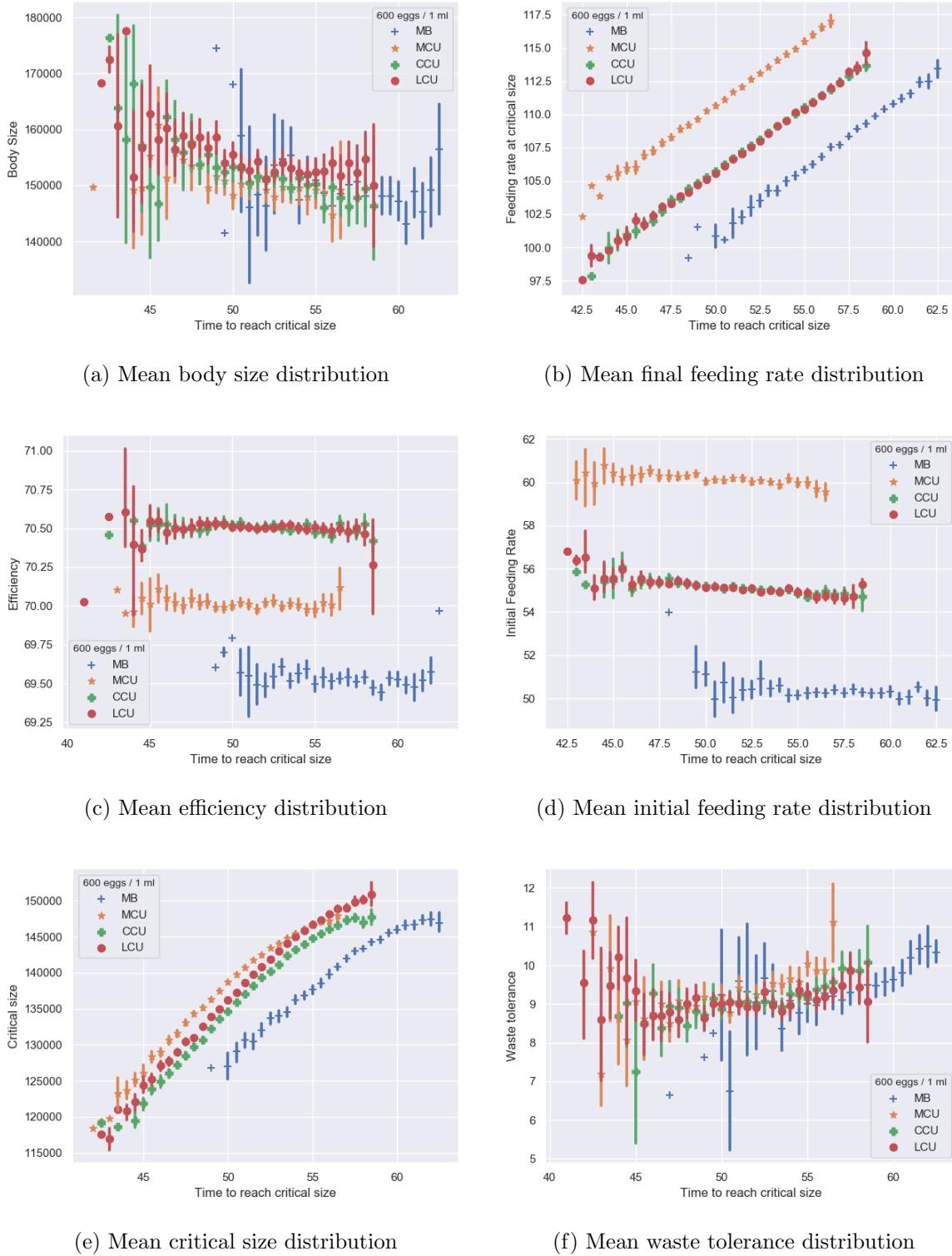


Figure 6.2: Mean trait value distribution of MB, MCU, CCU and LCU populations in 600 eggs / 1.5 ml density at 50<sup>th</sup> generation (errorbars represent 95% CI)

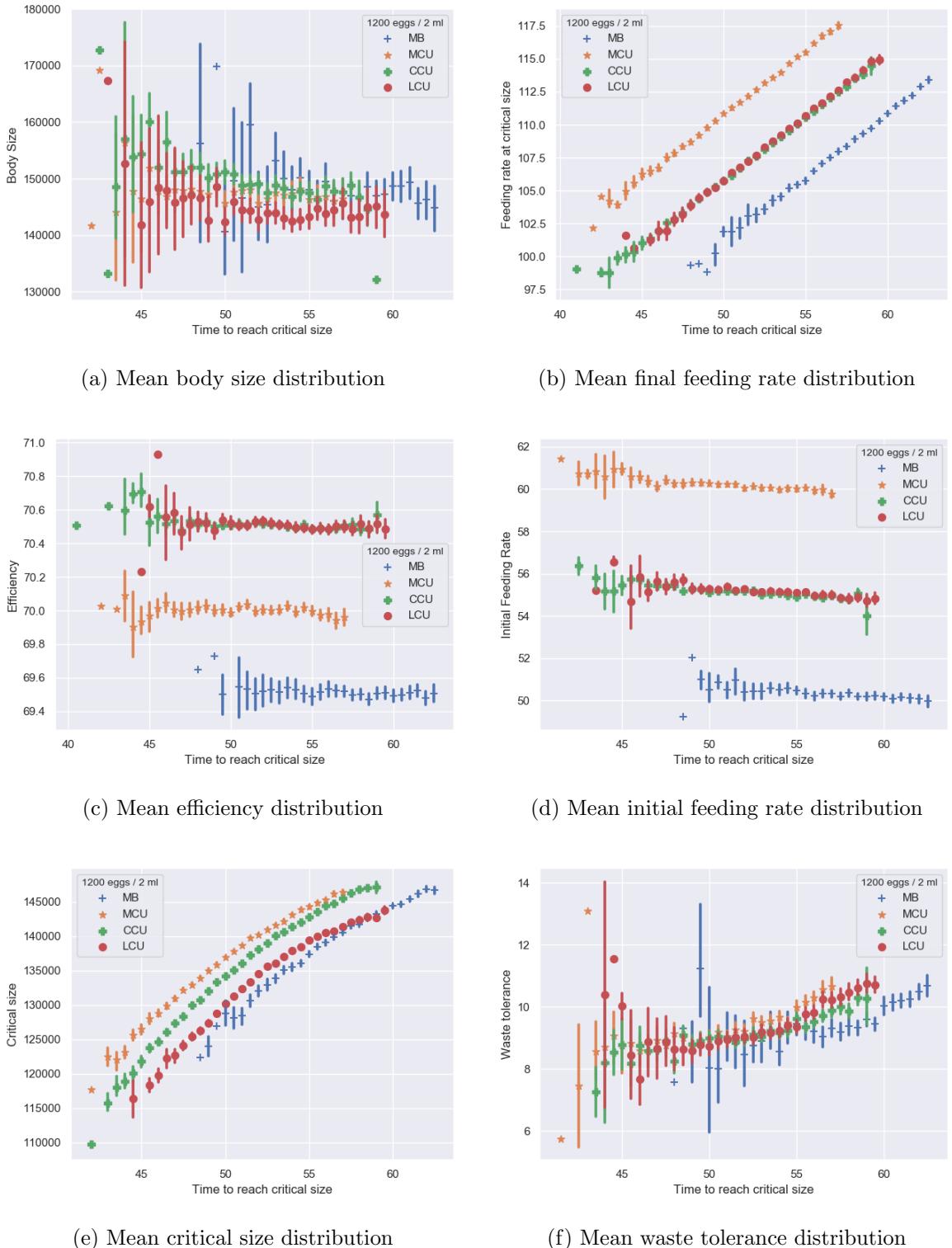


Figure 6.3: Mean trait value distribution of MB, MCU, CCU and LCU populations in 1200 eggs / 3 ml density at 50<sup>th</sup> generation (errorbars represent 95% CI)

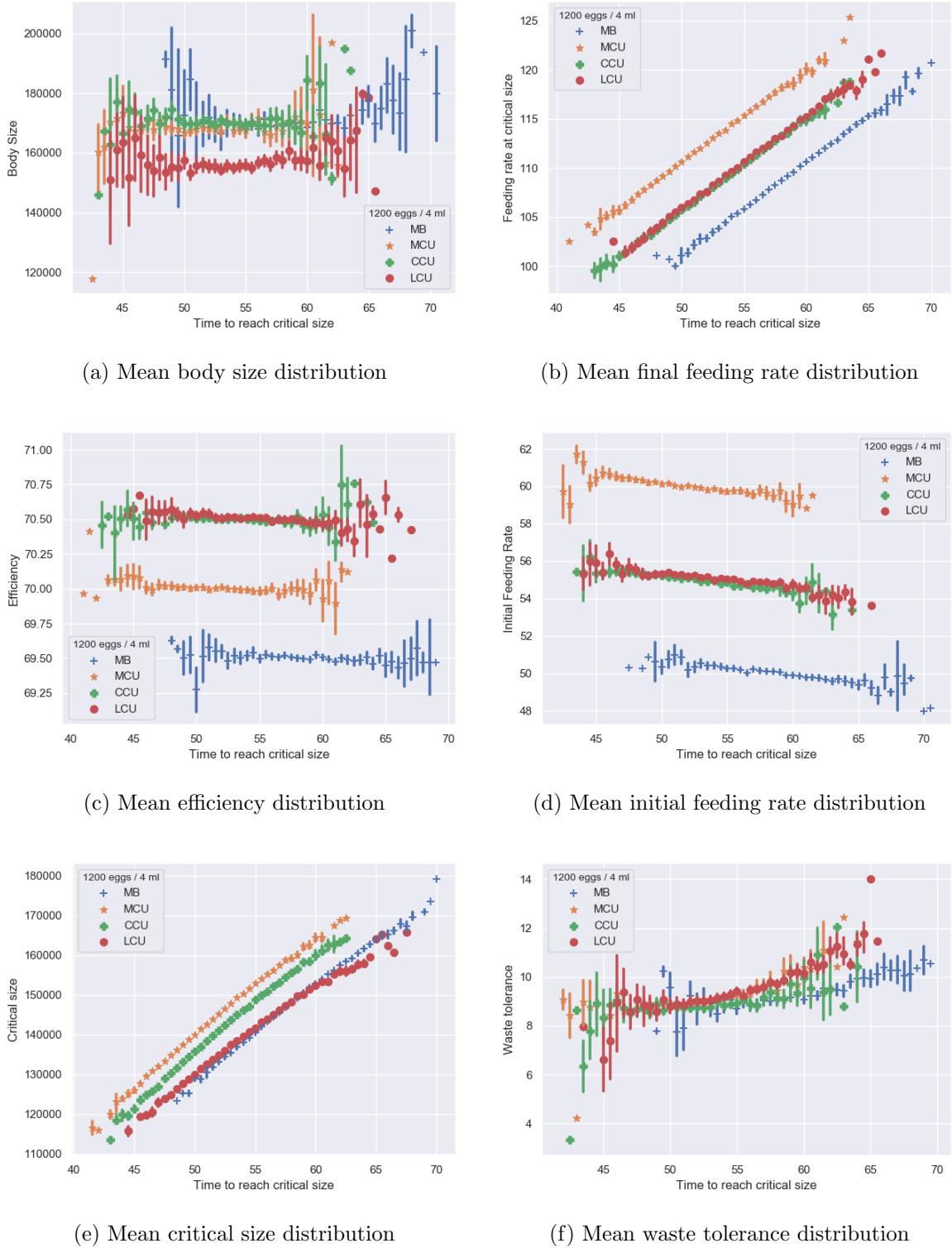


Figure 6.4: Mean trait value distribution of MB, MCU, CCU and LCU populations in 1200 eggs / 6 ml density at 50<sup>th</sup> generation (errorbars represent 95% CI)

## 6.2 Effects of Negative Correlation between Feeding Rate and Efficiency

From the mean trait distribution results, the effect of mean initial feeding rate distribution on body size distribution is clear (fig 6.3 and fig 6.4). If initial feeding rate is negatively correlated with development time, then the model would give a U-shaped body size distribution found in the larval crowded populations (ref). To understand further how these correlation between larval competitive traits would affect other life-history traits, I considered a negative correlation between initial feeding rate and efficiency in my model. Efficiency is derived at each generation from the distribution of initial feeding rate. It is given as:

$$\epsilon_i = K_\epsilon - x_6 * fr_i$$

Here,  $\epsilon_i$ : efficiency of  $i^{th}$  larva;

$fr_i$ : initial feeding rate of  $i^{th}$  larva;

$x_6$ : scaling parameter;

$K_\epsilon$ : Maximum value of efficiency (constant).

Using this correlation, timeseries was run for initial conditions given in table (no.) and same simulations as previous section were performed (replicate=5). The results show negative correlation of initial feeding rate across all populations at all four densities (see fig 6.5). Due to forced negative correlation between initial feeding rate and efficiency, mean efficiency distribution shows that late developing ones have higher efficiency (see fig 6.6). Fig 6.7 shows that final feeding rate is higher for late developing larvae even if their efficiency is higher and initial feeding rate is lower across all populations at all densities. Fig 6.8 was plotted with higher replicates ( $n=15$ ) to obtain a clear visualization. Here MCU, CCU and LCU population have mean body size first decreasing then increasing and decreasing variation wrt development time in MB and CCU culture. Such pattern is not visible in MB and LCU culture.

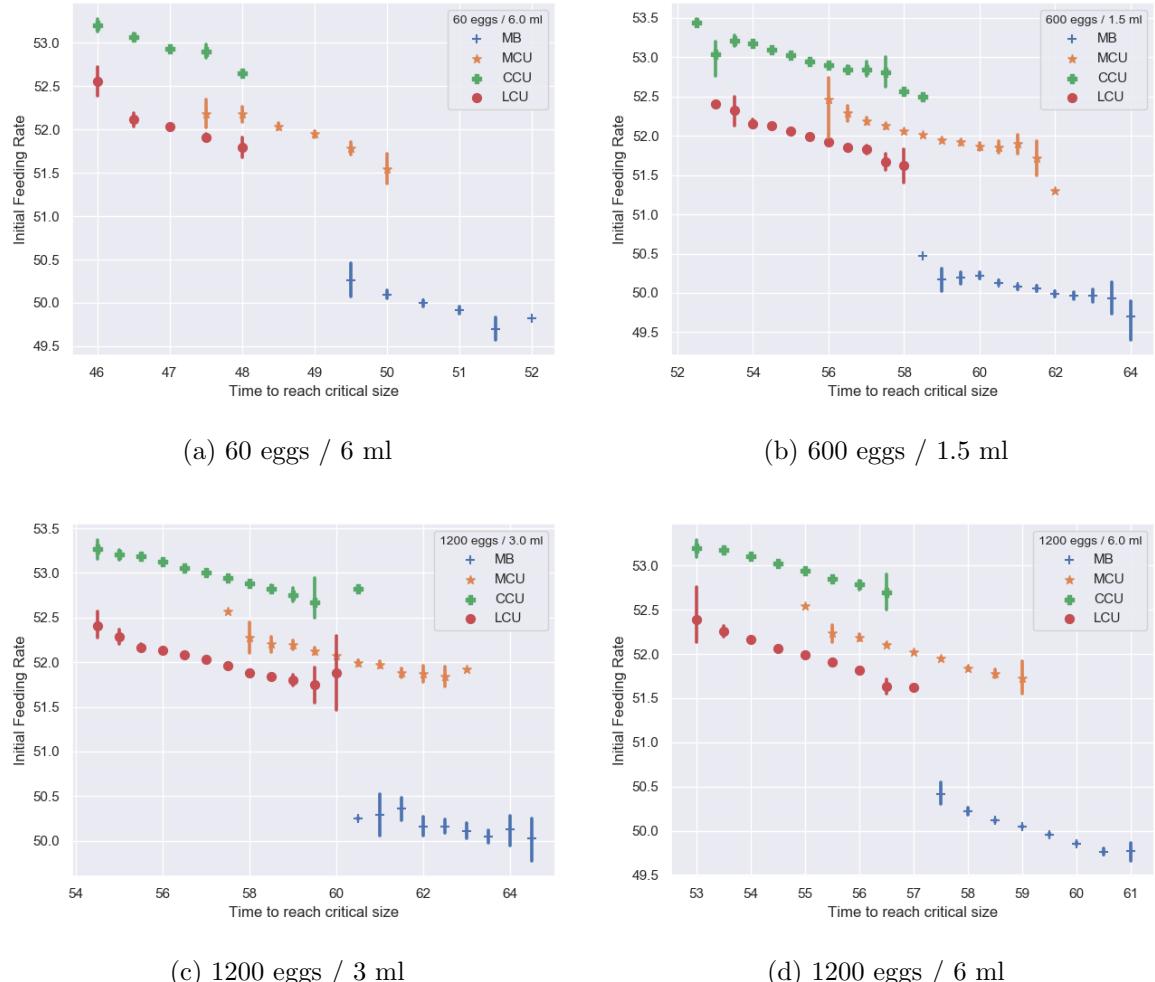


Figure 6.5: Mean initial feeding rate distribution of MB, MCU, CCU and LCU populations in (a) 60 eggs / 6 ml, (b) 600 eggs / 1.5 ml, (c) 1200 eggs / 3 ml and (d) 1200 eggs / 6 ml densities (errorbars represent 95% CI)

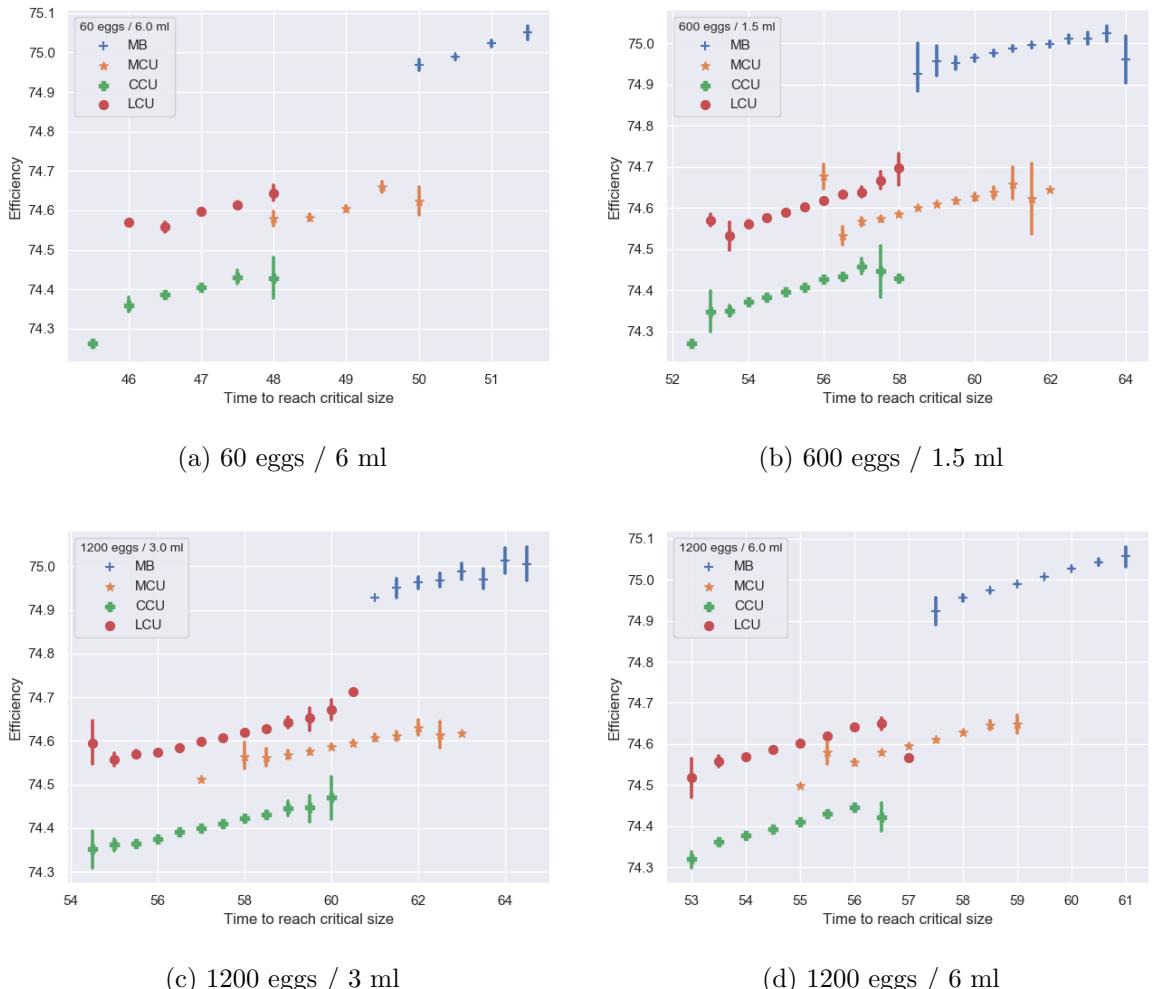
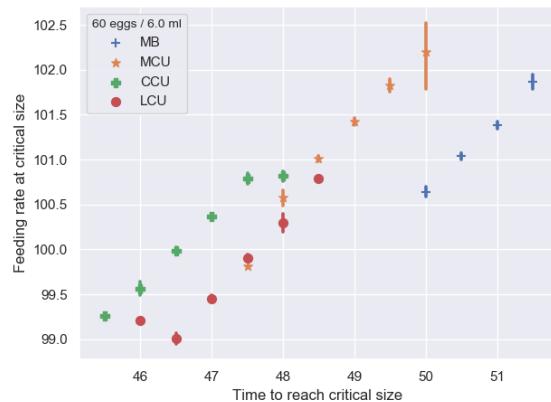
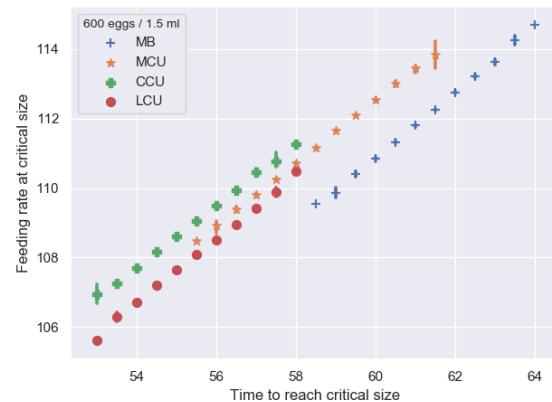


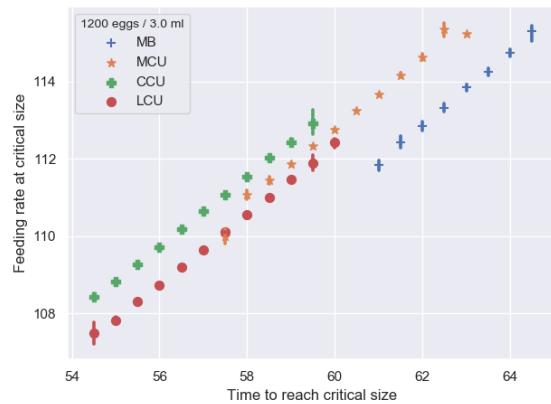
Figure 6.6: Mean efficiency distribution of MB, MCU, CCU and LCU populations in (a) 60 eggs / 6 ml, (b) 600 eggs / 1.5 ml, (c) 1200 eggs / 3 ml and (d) 1200 eggs / 6 ml densities (errorbars represent 95% CI)



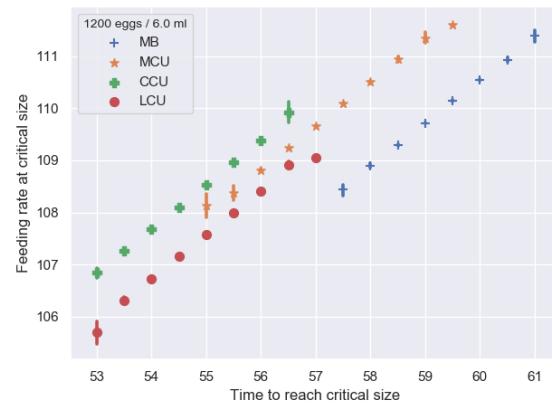
(a) 60 eggs / 6 ml



(b) 600 eggs / 1.5 ml



(c) 1200 eggs / 3 ml



(d) 1200 eggs / 6 ml

Figure 6.7: Mean feeding rate at critical size of MB, MCU, CCU and LCU populations in (a) 60 eggs / 6 ml, (b) 600 eggs / 1.5 ml, (c) 1200 eggs / 3 ml and (d) 1200 eggs / 6 ml densities (errorbars represent 95% CI)

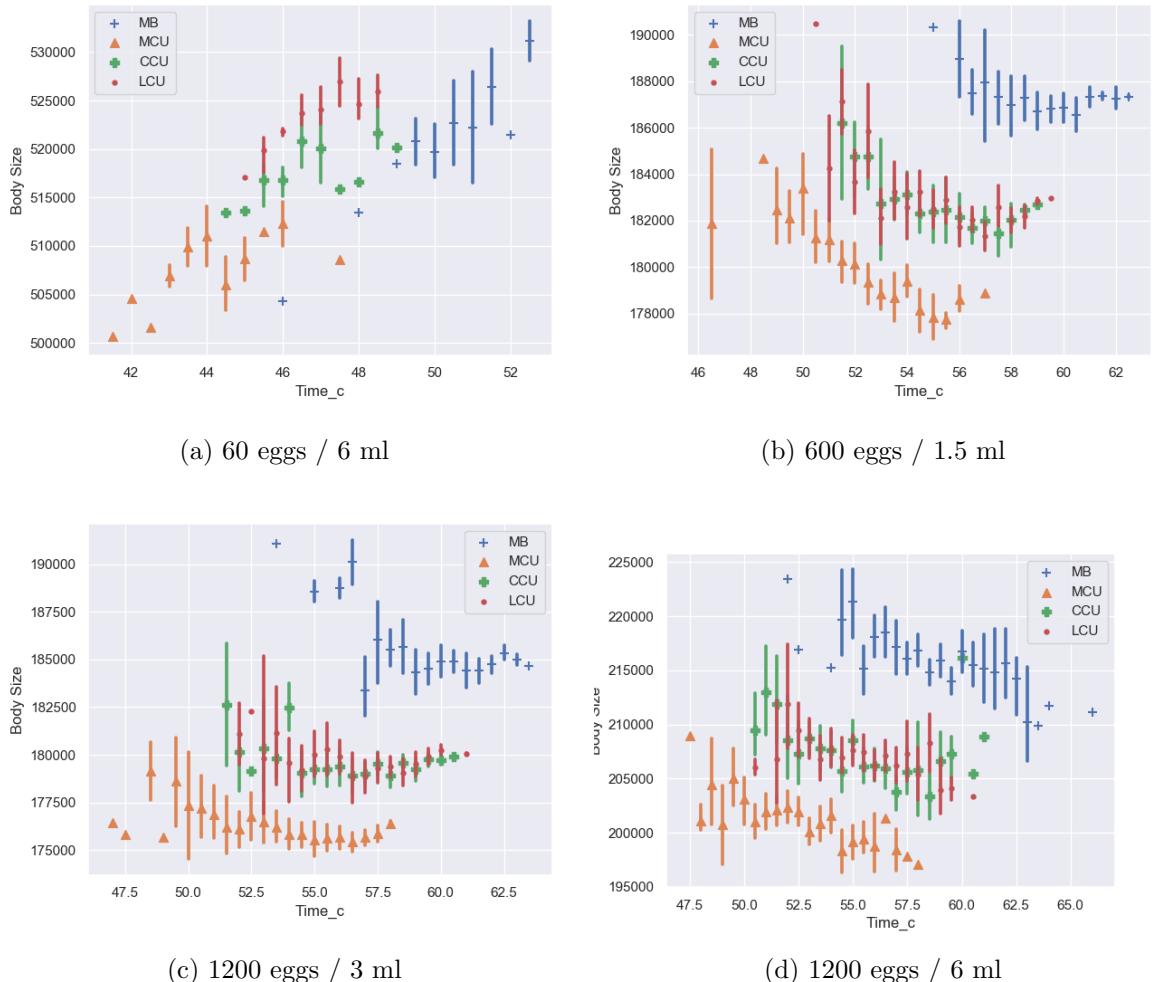


Figure 6.8: Mean efficiency distribution of MB, MCU, CCU and LCU populations in (a) 60 eggs / 6 ml, (b) 600 eggs / 1.5 ml, (c) 1200 eggs / 3 ml and (d) 1200 eggs / 6 ml densities (errorbars represent 95% CI)



# **Chapter 7**

## **Discussion**



# References

- Anderson, W. W., & Arnold, J. (1983). Density-Regulated Selection with Genotypic Interactions. *The American Naturalist*, 121(5), 649–655. doi:10.1086/284092
- Asmussen, M. A. (1983). Density-Dependent Selection Incorporating Intraspecific Competition. Ii. a Diploid Model. *Genetics*, 103(2), 335–350.
- Bakker, K. (1962). An Analysis of Factors Which Determine Success in Competition for Food Among Larvae of *Drosophila Melanogaster*. *Archives Néerlandaises de Zoologie*, 14(2), 200–281. doi:10.1163/036551661X00061
- Borash, D. J. [D. J.], & Ho, G. T. (2001). Patterns of selection: Stress resistance and energy storage in density-dependent populations of *Drosophila melanogaster*. *Journal of Insect Physiology*, 47(12), 1349–1356. doi:10.1016/S0022-1910(01)00108-1
- Borash, D. J. [Daniel J.], Gibbs, A. G., Joshi, A., & Mueller, L. D. (1998). A Genetic Polymorphism Maintained by Natural Selection in a Temporally Varying Environment. *The American Naturalist*, 151(2), 148–156. doi:10.1086/286108
- Burnet, B., Sewell, D., & Bos, M. (1977). Genetic analysis of larval feeding behaviour in *Drosophila melanogaster*: II. Growth relations and competition between selected lines. *Genetics Research*, 30(2), 149–161. doi:10.1017/S0016672300017559
- Case, T. J. (2000). *An Illustrated Guide to Theoretical Ecology*. Oxford University Press.
- Clarke, B. (1972). Density-Dependent Selection. *The American Naturalist*, 106(947), 1–13. doi:10.1086/282747
- Dey, S., Bose, J., & Joshi, A. (2012). Adaptation to larval crowding in *Drosophila ananassae* leads to the evolution of population stability. *Ecology and Evolution*, 2(5), 941–951. eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1002/ece3.227>. doi:10.1002/ece3.227

- Godoy-Herrera, R. (1977). Inter- and intrapopulational variation in digging in *Drosophila melanogaster* larvae. *Behavior Genetics*, 7(6), 433–439. doi:10.1007/BF01066778
- Joshi, A., Knight, C. D., & Mueller, L. D. (1996). Genetics of larval urea tolerance in *Drosophila melanogaster*. *Heredity*, 77(1), 33–39. doi:10.1038/hdy.1996.105
- Joshi, A., & Mueller, L. D. (1988). Evolution of Higher Feeding Rate in *Drosophila* Due to Density-Dependent Natural Selection. *Evolution*, 42(5), 1090–1093. doi:10.2307/2408924
- Joshi, A., & Mueller, L. D. (1993). Directional and Stabilizing Density-Dependent Natural Selection for Pupation Height in *Drosophila Melanogaster*. *Evolution*, 47(1), 176–184. \_eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1558-5646.1993.tb01208.x>. doi:10.1111/j.1558-5646.1993.tb01208.x
- Joshi, A., & Mueller, L. D. (1996). Density-dependent natural selection in *Drosophila*: Trade-offs between larval food acquisition and utilization. *Evolutionary Ecology*, 10(5), 463–474. doi:10.1007/BF01237879
- Joshi, A., Prasad, N. G., & Shakarad, M. (2001). K-selection,  $\alpha$ -selection, effectiveness, and tolerance in competition: Density-dependent selection revisited. *Journal of Genetics*, 80(2), 63–75. doi:10.1007/BF02728332
- MacArthur, R. H. (1962). SOME GENERALIZED THEOREMS OF NATURAL SELECTION. *Proceedings of the National Academy of Sciences of the United States of America*, 48(11), 1893–1897.
- MacArthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press.
- Mueller, L. D. (1990). Density-dependent natural selection does not increase efficiency. *Evolutionary Ecology*, 4(4), 290–297. doi:10.1007/BF02270928
- Mueller, L. D. (1997). Theoretical and Empirical Examination of Density-Dependent Selection. *Annual Review of Ecology and Systematics*, 28(1), 269–288. \_eprint: <https://doi.org/10.1146/annurev.ecolsys.28.1.269>. doi:10.1146/annurev.ecolsys.28.1.269
- Mueller, L. D., & Ayala, F. J. (1981). Trade-off between r-selection and K-selection in *Drosophila* populations. *Proceedings of the National Academy of Sciences*, 78(2), 1303–1305. doi:10.1073/pnas.78.2.1303

- Nagarajan, A., Natarajan, S. B., Jayaram, M., Thammanna, A., Chari, S., Bose, J., ... Joshi, A. (2016). Adaptation to larval crowding in *Drosophila ananassae* and *Drosophila nasuta nasuta*: Increased larval competitive ability without increased larval feeding rate. *Journal of Genetics*, 95(2), 411–425. doi:10.1007/s12041-016-0655-9
- Prasad, N. G., & Joshi, A. (2003). What have two decades of laboratory life-history evolution studies on *Drosophila melanogaster* taught us? *Journal of Genetics*, 82(1), 45–76. doi:10.1007/BF02715881
- Roughgarden, J. (1971). Density-Dependent Natural Selection. *Ecology*, 52(3), 453–468. \_eprint: <https://esajournals.onlinelibrary.wiley.com/doi/pdf/10.2307/1937628>. doi:10.2307/1937628
- Santos, M., Borash, D. J., Joshi, A., Bounlutay, N., & Mueller, L. D. (1997). Density-Dependent Natural Selection in *Drosophila*: Evolution of Growth Rate and Body Size. *Evolution*, 51(2), 420–432. \_eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1558-5646.1997.tb02429.x> doi:10.1111/j.1558-5646.1997.tb02429.x
- Sarangi, M. (2013). *Preliminary investigations into the causes for alternative routes to the evolution of competitive ability in populations of drosophila selected for adaptation to larval crowding* (Thesis, Jawaharlal Nehru Centre for Advanced Scientific Research). Accepted: 2014-11-21T12:30:56Z.
- Sarangi, M. (2018). *Ecological details mediate different paths to the evolution of larval competitive ability in Drosophila* (Thesis, Jawaharlal Nehru Centre for Advanced Scientific Research (JNCASR)). Accepted: 2019-07-26T10:33:37Z.
- Sarangi, M., Nagarajan, A., Dey, S., Bose, J., & Joshi, A. (2016). Evolution of increased larval competitive ability in *Drosophila melanogaster* without increased larval feeding rate. *Journal of Genetics*, 95(3), 491–503. doi:10.1007/s12041-016-0656-8
- Shiotsugu, J., Leroi, A. M., Yashiro, H., Rose, M. R., & Mueller, L. D. (1997). The Symmetry of Correlated Selection Responses in Adaptive Evolution: An Experimental Study Using *Drosophila*. *Evolution*, 51(1), 163–172. \_eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1558-5646.1997.tb02397.x> doi:10.1111/j.1558-5646.1997.tb02397.x

Testa, N. D., Ghosh, S. M., & Shingleton, A. W. (2013). Sex-Specific Weight Loss Mediates Sexual Size Dimorphism in *Drosophila melanogaster*. *PLoS ONE*, 8(3). doi:10.1371/journal.pone.0058936

# Appendix A

## Tables

This appendix contains values of all paramters used in the simulations.

### A.1 Larval Trait Parameters

No.	Larval Trait	Symbol	Distribution
1.	Initial feeding rate		$N(,)$
2.	Critical size		$N(,)$
3.	Efficiency		$N(,)$
4.	Waste tolerance		$N(,)$

Table A.1: Distributions and values of larval trait parameters used for initiating the model

### A.2 Scaling Parameters

No.	Paramter	Value
1.	$x_1$	0.017
2.	$x_2$	1e4

Table A.2: Values of scaling parameters used in the model

### A.3 Other Larval Parameters

No.	Paramter	Symbol	Value
1.	Larval food (1.5 ml)	$food$	1.85e8
2.	Initial body size ( $t=0$ )	$S_i(0)$	3.0
3.	Proportion of waste diffusion	$k_d$	0.12
4.	Feeding band size	$fband$	7.4e9
5.	Diffusion band size	$dband$	7.4e9
6.	Volume of food (pre-critical)	$V_f(pre)$	1.0

Table A.3: Values of larval parameters used for initiating the model