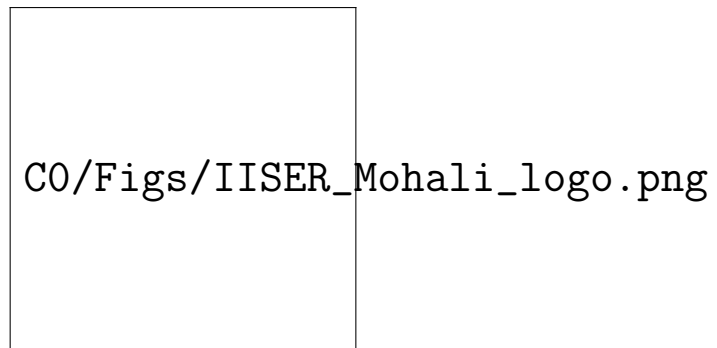


# Moran Model

Manu M.

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



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

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I hereby declare that this thesis and the work reported herein was composed by and originated entirely from me. Information derived from the published and unpublished work of others has been acknowledged in the text and references are given in the list of sources.

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## Abstract

# Chapter 1

## Introduction

# References

# Chapter 2

## Preliminaries

### 2.1 Moran Model

We consider one of the most significant work on Markov chain modelling in population genetics. The following model was proposed by P. A. P. Moran in 1958.

#### 2.1.1 Model Dynamics

We consider a haploid population with two genotypes  $A$  and  $a$ . This model envisages to follow population through its birth-death events. Precisely, the new generation is formed from the old generation in a certain manner.

From the existing population, one individual is chosen randomly to give birth and the offspring would be of the same genotype. At the same time, one randomly chosen individual from the old population dies. Therefore, the population size remains constant. We denote it by  $N$ . Also, we denote by  $X_n$ , the number of  $A$  genes in the  $n$ th generation. By  $n$ th generation, we understand that population has undergone  $n$  birth-death events. We want to study the Markov chain  $(X_n)_{n \geq 0}$ , which has state space  $0, 1, \dots, N$ .

## 2.2 Markov Chains

### 2.2.1 Basic Definitions and Properties

Markov chains often describe the movements of a system between various states. In this paper, we will discuss *discrete-time* Markov chains, meaning that at each step our system can either stay in the state it is in or change to another state. We denote the random variable  $X_n$  as a sort of marker of what state our system is in at step  $n$ .  $X_n$  can take the value of any  $i \in I$ , where each  $i$  is a *state* in the *state-space*,  $I$ . States are usually just denoted as numbers and our state-space as a countable set.

We will call  $\lambda = (\lambda_{i1}, \lambda_{i2}, \dots) = (\lambda_i, |, i \in I)$  the *probability distribution* on  $X_n$  if:  $\lambda_i = P(X_n = i)$  and  $\sum_{i \in I} \lambda_i = 1$ . Also, a matrix  $P = \{p_{ij}\}$ , where  $i, j \in I$ , is called *stochastic* if  $\sum_{j \in I} \lambda_{ij} = 1, \forall i \in I$ , i.e. every row of the matrix is a distribution. Now we can define a Markov chain explicitly.

**Definitions 1**  $(X_0, X_1, \dots) = (X_n)_{n \geq 0}$  is a Markov chain with initial distribution  $\lambda$  and transition matrix  $P$ , shortened to  $\text{Markov}(\lambda, P)$ , if

- $\lambda$  is the probability distribution on  $X_0$ ;
- given that  $X_n = i$ ,  $(p_{ij} | i, j \in I)$  is the probability distribution on  $X_{n+1}$  and is independent of  $X_k, 0 \leq k < n$ , i.e.  $P(X_{n+1} = j | X_n = i) = p_{ij}$ .

**Theorem 2.2.1**  $(X_n)_{0 \leq n \leq N}$  is  $\text{Markov}(\lambda, P)$  if and only if

$$P(X_0 = i_0, X_1 = i_1, \dots, X_N = i_N) = \lambda_{i_0} p_{i_0 i_1} p_{i_1 i_2} \cdots p_{i_{N-1} i_N}. \quad (2.1)$$

First, suppose  $(X_n)_{0 \leq n \leq N}$  is  $\text{Markov}(\lambda, P)$ , thus

$$\begin{aligned} & P(X_0 = i_0, X_1 = i_1, \dots, X_N = i_N) \\ &= P(X_0 = i_0) P(X_1 = i_1 | X_0 = i_0) \cdots P(X_N = i_N | X_0 = i_0, \dots, X_{N-1} = i_{N-1}) \\ &= P(X_0 = i_0) P(X_1 = i_1 | X_0 = i_0) \cdots P(X_N = i_N | X_{N-1} = i_{N-1}) \\ &= \lambda_{i_0} p_{i_0 i_1} p_{i_1 i_2} \cdots p_{i_{N-1} i_N} \end{aligned}$$

Now assume that (1.3) holds for  $N$ , thus

$$P(X_0 = i_0, X_1 = i_1, \dots, X_N = i_N) = \lambda_{i_0} p_{i_0 i_1} p_{i_1 i_2} \cdots p_{i_{N-1} i_N}$$

$$\begin{aligned}\sum_{i_N \in I} P(X_0 = i_0, X_1 = i_1, \dots, X_N = i_N) &= \sum_{i_N \in I} \lambda_{i_0} p_{i_0 i_1} p_{i_1 i_2} \cdots p_{i_{N-1} i_N} \\ P(X_0 = i_0, X_1 = i_1, \dots, X_{N-1} = i_{N-1}) &= \lambda_{i_0} p_{i_0 i_1} p_{i_1 i_2} \cdots p_{i_{N-2} i_{N-1}}\end{aligned}$$

And now by induction, (1.3) holds for all  $0 \leq n \leq N$ . From the formula for conditional probability, namely that  $P(A|B) = P(A \cap B)/P(B)$ , we can show that

$$\begin{aligned}P(X_{N+1} = i_{N+1} | X_0 = i_0, \dots, X_N = i_N) &= \frac{P(X_0 = i_0, \dots, X_N = i_N, X_{N+1} = i_{N+1})}{P(X_0 = i_0, \dots, X_N = i_N)} \\ &= \frac{\lambda_{i_0} p_{i_0 i_1} \cdots p_{i_{N-1} i_N} p_{i_N i_{N+1}}}{\lambda_{i_0} p_{i_0 i_1} \cdots p_{i_{N-1} i_N}} \\ &= p_{i_N i_{N+1}}\end{aligned}$$

Thus, by definition,  $(X_n)_{0 \leq n \leq N}$  is Markov( $\lambda, P$ ).

The next theorem emphasizes the memorylessness of Markov chains. In the formulation of this theorem, we use the idea of the *unit mass at  $i$* . It is denoted as  $\delta_i = (\delta_{ij})$  where

$$\delta_{ij} = \begin{cases} 1 & \text{if } i = j \\ 0 & \text{otherwise} \end{cases}$$

**Theorem 2.2.2** *Let  $(X_n)_{n \geq 0}$  be Markov( $\lambda, P$ ). Then, given that  $X_m = i$ ,  $(X_l)_{l \geq m}$  is Markov( $\delta_i, P$ ) and is independent of  $X_k$ ,  $0 \leq k < m$ .*

Let the event  $A = \{X_m = i_m, \dots, X_n = i_n\}$  and the event  $B$  be any event determined by  $X_0, \dots, X_m$ . To prove the theorem, we must show that

$$P(A \cap B | X_m = i) = \delta_{ii_m} p_{i_m i_{m+1}} \cdots p_{i_{n-1} i_n} P(B | X_m = i)$$

thus the result follows from Theorem 1.2. First, let us consider any elementary event

$$B = B_k = \{X_0 = i_0, \dots, X_m = i_m\}$$

Here we show that

$$P(A \cap B_k \text{ and } i = i_m | X_m = i) = \frac{\delta_{ii_m} p_{i_m i_{m+1}} \cdots p_{i_{n-1} i_n} P(B_k)}{P(X_m = i)}$$

which follows from Theorem 1.2 and the definition of conditional probability. Any event,  $B$ , determined by  $X_0, \dots, X_m$  can be written as a disjoint union of elementary events,  $B = \bigcup_{k=1}^{\infty} B_k$ . Thus, we can prove our above identity by summing up all of the different  $B_k$  for any given event.

An additional idea that is going to be important later is the idea of conditioning on the initial state,  $X_0$ . We will let  $P(A | X_0 = i) = P_i(A)$ . Similarly, we will let  $E(A | X_0 = i) = E_i(A)$ .

## 2.2.2 Stopping Times and the Strong Markov Property

We start this section with the definition of a stopping time.

**Definitions 2** A random variable  $T$  is called a stopping time if the event  $\{T = n\}$  depends only on  $X_0, \dots, X_n$  for  $n = 0, 1, 2, \dots$

An example of a stopping time would be the *first passage time*

$$T_i = \inf\{n \geq 1 \mid X_n = i\}.$$

where we define  $\inf \emptyset = \infty$ . This is a stopping time since  $\{T_i = n\} = \{X_k \neq i, X_n = i \mid 0 < k < n\}$ . Now we will define an expansion of this idea that we will use later.

**Definitions 3** The  $r$ th passage time  $T_i^{(r)}$  to state  $i$  is defined recursively using the first passage time.

$$T_i^{(0)} = 0, \quad T_i^{(1)} = T_i$$

and, for  $r = 1, 2, \dots$ ,

$$T_i^{(r+1)} = \inf\{n \geq T_i^{(r)} + 1 \mid X_n = i\}.$$

This leads to the natural definition of the *length of the  $r$ th excursion* to  $i$  as

$$S_i^{(r)} = \begin{cases} T_i^{(r)} - T_i^{(r-1)} & \text{if } T_i^{(r-1)} < \infty \\ 0 & \text{otherwise.} \end{cases}$$

The following theorem shows how the Markov property holds at stopping times.

**Theorem 2.2.3** Let  $T$  be a stopping time of  $(X_n)_{n \geq 0}$  which is Markov( $\lambda, P$ ). Then given  $T < \infty$  and  $X_T = i$ ,  $(X_l)_{l \geq T}$  is Markov( $\delta_i, P$ ) and independent of  $X_k$ ,  $0 \leq k < T$ .

First, we already have that  $(X_l)_{l \geq T}$  is Markov( $\delta_i, P$ ) by Theorem 1.4, so we just need to show the independence condition. Let the event  $A = \{X_T = i_0, \dots, X_{T+n} = i_n\}$  and the event  $B$  be any event determined by  $X_0, \dots, X_T$ . It is important to notice that the event  $B \cap \{T = m\}$  is determined by  $X_0, \dots, X_m$ . We get that

$$P(A \cap B \cap \{T = m\} \cap \{X_T = i\}) = P_i(X_0 = i_0, \dots, X_n = i_n)P(B \cap \{T = m\} \cap \{X_T = i\})$$

If we now sum over  $m = 0, 1, 2, \dots$  and divide each side by  $P(T < \infty, X_T = i)$  using the definition of conditional probability, we obtain

$$P(A \cap B | T < \infty, X_T = i) = P_i(X_0 = i_0, \dots, X_n = i_n)P(B | T < \infty, X_T = i)$$

which gives us the independence we desired.

### 2.2.3 Recurrence and Transience

**Definitions 4** Let  $(X_n)_{n \geq 0}$  be Markov with transition matrix  $P$ . We say that a state  $i$  is recurrent if

$$P_i(X_n = i \text{ for infinitely many } n) = 1,$$

and we say that a state  $i$  is transient if

$$P_i(X_n = i \text{ for infinitely many } n) = 0.$$

The following results allow us to show that any state is necessarily either recurrent or transient.

**Lemma 2.2.1** For  $r = 2, 3, \dots$ , given that  $T_i^{(r-1)} < \infty$ ,  $S_i^{(r)}$  is independent of  $X_k, 0 \leq k \leq T_i^{(r-1)}$  and

$$P(S_i^{(r)} = n | T_i^{(r-1)} < \infty) = P_i(T_i = n).$$

We can directly apply Theorem 2.3 where  $T_i^{(r-1)}$  is the stopping time  $T$ , since it is assured that  $X_T = i$  when  $T < \infty$ . So, given that  $T_i^{(r-1)} < \infty$ ,  $(X_l)_{l \geq T}$  is Markov( $\delta_i, P$ ) and independent of  $X_k, 0 \leq k < T$ , the independence wanted. Yet, we know

$$S_i^{(r)} = \inf\{l - T \geq 1 | X_l = i\}$$

so  $S_i^{(r)}$  is the first passage time of  $(X_l)_{l \geq T}$  to state  $i$ , giving us our desired equality.

**Definitions 5** The idea of the number of visits to  $i$ ,  $V_i$ , is intuitive and can be easily defined using the indicator function

$$V_i = \sum_{n=0}^{\infty} 1_{\{X_n=i\}}$$

A nice property of  $V_i$  is that

$$E_i(V_i) = E_i\left(\sum_{n=0}^{\infty} 1_{\{X_n=i\}}\right) = \sum_{n=0}^{\infty} E_i(1_{\{X_n=i\}}) = \sum_{n=0}^{\infty} P_i(X_n = i).$$



**Definitions 6** *Another intuitive and useful term is the return probability to  $i$ , defined as*

$$f_i = P_i(T_i < \infty).$$

**Lemma 2.2.2**  $P_i(V_i > r) = (f_i)^r$  for  $r = 0, 1, 2, \dots$ .

First, we know that our claim is necessarily true when  $r = 0$ . Thus, we can use induction and the fact that if  $X_0 = i$  then  $\{V_i > r\} = \{T_i^{(r)} < \infty\}$  to conclude that

$$\begin{aligned} P_i(V_i > r + 1) &= P_i(T_i^{(r+1)} < \infty) \\ &= P_i(T_i^{(r)} < \infty \text{ and } S_i^{(r+1)} < \infty) \\ &= P_i(S_i^{(r+1)} < \infty \mid T_i^{(r)} < \infty) P_i(T_i^{(r)} < \infty) \\ &= f_i \cdot (f_i)^r = (f_i)^{r+1} \end{aligned}$$

using Lemma 3.2, so our claim is true for all  $r$ .

**Theorem 2.2.4** *The following two cases hold and show that any state is either recurrent or transient:*

1. if  $P_i(T_i < \infty) = 1$ , then  $i$  is recurrent and  $\sum_{n=0}^{\infty} P_i(X_n = i) = \infty$ ;
2. if  $P_i(T_i < \infty) < 1$ , then  $i$  is transient and  $\sum_{n=0}^{\infty} P_i(X_n = i) < \infty$ .

If  $P_i(T_i < \infty) = f_i = 1$  by Lemma 3.5, then

$$P_i(V_i = \infty) = \lim_{r \rightarrow \infty} P_i(V_i > r) = \lim_{r \rightarrow \infty} 1^r = 1$$

so  $i$  is recurrent and

$$\sum_{n=0}^{\infty} P_i(X_n = i) = E_i(V_i) = \infty.$$

In the other case,  $f_i = P_i(T_i < \infty) < 1$  then using our fact about  $V_i$

$$\begin{aligned} \sum_{n=0}^{\infty} P_i(X_n = i) &= E_i(V_i) = \sum_{n=1}^{\infty} n P_i(V_i = n) = \sum_{n=1}^{\infty} \sum_{r=0}^{n-1} P_i(V_i = n) \\ &= \sum_{r=0}^{\infty} \sum_{n=r+1}^{\infty} P_i(V_i = n) = \sum_{r=0}^{\infty} P_i(V_i > r) = \sum_{r=0}^{\infty} (f_i)^r = \frac{1}{1 - f_i} < \infty \end{aligned}$$

so  $P_i(V_i = \infty) = 0$  and  $i$  is transient.

## 2.2.4 Communication Classes and Recurrence

**Definitions 7** State  $i$  can send to state  $j$ , and we write  $i \rightarrow j$  if

$$P_i(X_n = j \text{ for some } n \geq 0) > 0.$$

Also  $i$  communicates with  $j$ , and we write  $ij$  if both  $i \rightarrow j$  and  $j \rightarrow i$ .

**Theorem 2.2.5** For distinct states  $i, j \in I$ ,  $i \rightarrow j \iff p_{ii_1}p_{i_1i_2} \cdots p_{i_{n-1}j} > 0$  for some states  $i_1, i_2, \dots, i_{n-1}$ . Also,  $\sim$  is an equivalence relation on  $I$ .

()

$$0 < P_i(X_n = j \text{ for some } n \geq 0) \leq \sum_{n=0}^{\infty} P_i(X_n = j) = \sum_{n=0}^{\infty} \sum_{i_1, \dots, i_{n-1}} p_{ii_1}p_{i_1i_2} \cdots p_{i_{n-1}j}$$

Thus, for some  $p_{ii_1}p_{i_1i_2} \cdots p_{i_{n-1}j} > 0$  for some states  $i_1, i_2, \dots, i_{n-1}$ .

() Take some  $i_1, i_2, \dots, i_{n-1}$  such that

$$0 < p_{ii_1}p_{i_1i_2} \cdots p_{i_{n-1}j} \leq P_i(X_n = j) \leq P_i(X_n = j \text{ for some } n \geq 0).$$

Now it is clear from the proven inequality that  $i \rightarrow j, j \rightarrow ki \rightarrow k$ . Also, it is true that  $ii$  for any state  $i$  and that  $ijji$ . Thus,  $\sim$  is an equivalence relation on  $I$ .

**Definitions 8** We say that partitions  $I$  into communication classes. Also, a Markov chain or transition matrix  $P$  where  $I$  is a single communication class is called irreducible.

**Theorem 2.2.6** Let  $C$  be a communication class. Either all states in  $C$  are recurrent or all are transient.

Take any distinct pair of states  $i, j \in C$  and suppose that  $i$  is transient. Then there exist  $n, m \geq 0$  such that  $P_i(X_n = j) > 0$  and  $P_j(X_m = i) > 0$ , and for all  $r \geq 0$

$$P_i(X_{n+r+m} = i) \geq P_i(X_n = j)P_j(X_r = j)P_j(X_m = i).$$

This implies that

$$\sum_{r=0}^{\infty} P_j(X_r = j) \leq \frac{1}{P_i(X_n = j)P_j(X_m = i)} \sum_{r=0}^{\infty} P_i(X_{n+r+m} = i) < \infty$$

by Theorem 3.6. So any arbitrary  $j$  is transient, again by Theorem 3.6, so the whole of  $C$  is transient. The only way for this not to be true is if all states in  $C$  are recurrent. This theorem shows us that recurrence and transience is a class property, and we will refer to it in the future as such.

**Theorem 2.2.7** *Suppose  $P$  is irreducible and recurrent. Then for all  $i \in I$  we have  $P(T_i < \infty) = 1$ .*

By Theorem 2.3 we have

$$P(T_i < \infty) = \sum_{j \in I} P_j(T_i < \infty) P(X_0 = j)$$

so we only need to show  $P_j(T_i < \infty) = 1$  for all  $j \in I$ . By the irreducibility of  $P$ , we can pick an  $m$  such that  $P_i(X_m = j) > 0$ . From Theorem 3.6, we have

$$\begin{aligned} 1 &= P_i(X_n = i \text{ for infinitely many } n) \\ &= P_i(X_n = i \text{ for some } n \geq m + 1) \\ &= \sum_{k \in I} P_i(X_n = i \text{ for some } n \geq m + 1 \mid X_m = k) P_i(X_m = k) \\ &= \sum_{k \in I} P_k(T_i < \infty) P_i(X_m = k) \end{aligned}$$

using Theorem 2.3 again. Since  $\sum_{k \in I} P_i(X_m = k) = 1$  so we have that  $P_j(T_i < \infty) = 1$ .

# 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.

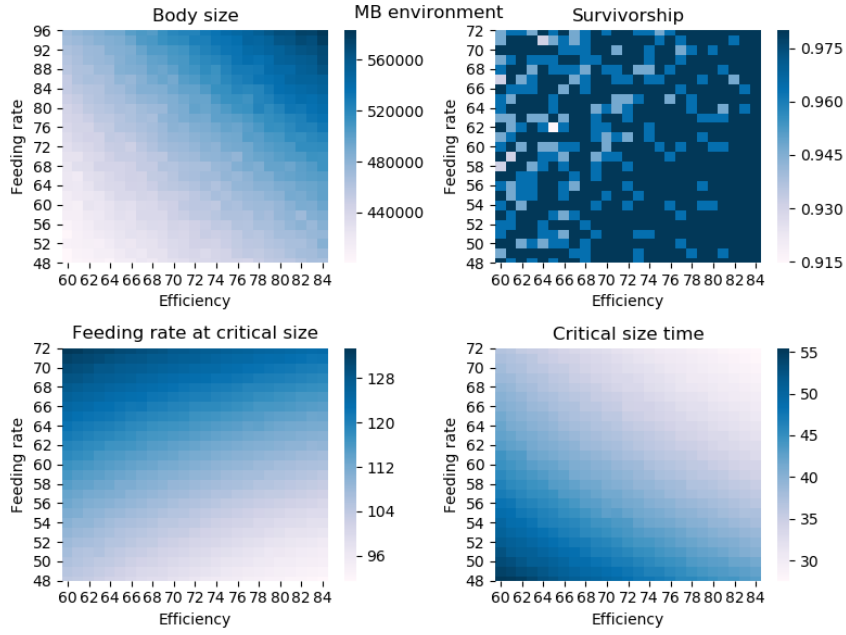


Figure 3.1: Effect of initial feeding rate and efficiency on larval traits in MB culture

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.

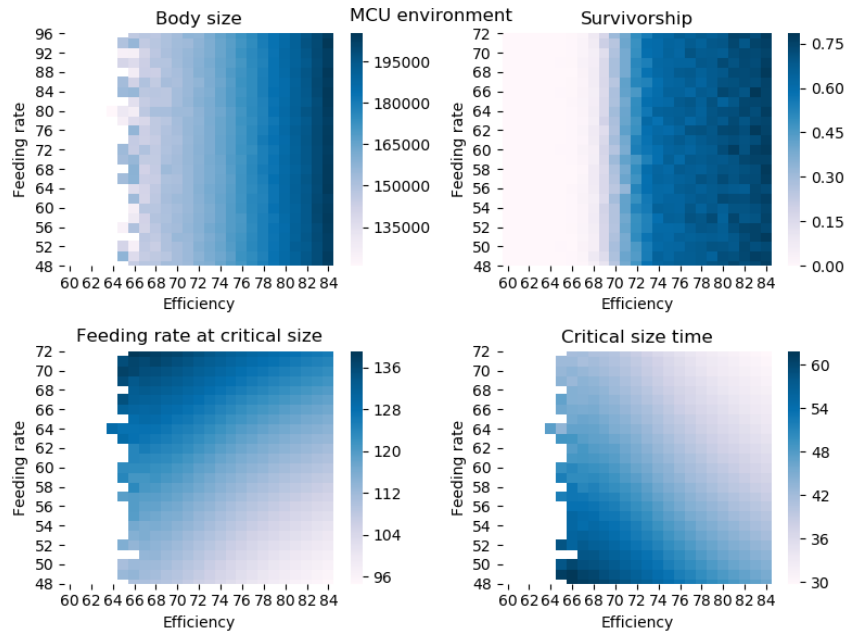


Figure 3.2: Effect of initial feeding rate and efficiency on larval traits in MCU culture

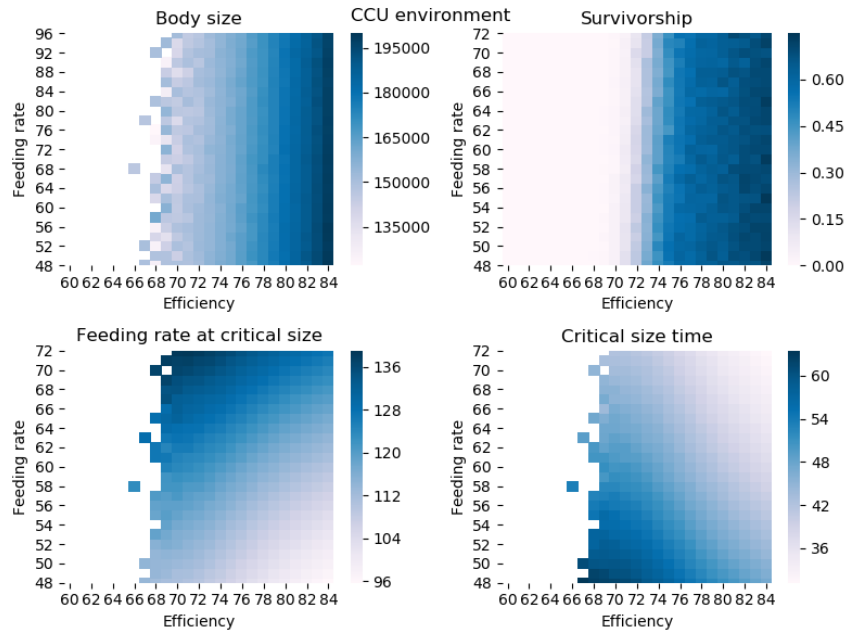


Figure 3.3: Effect of initial feeding rate and efficiency on larval traits in CCU culture

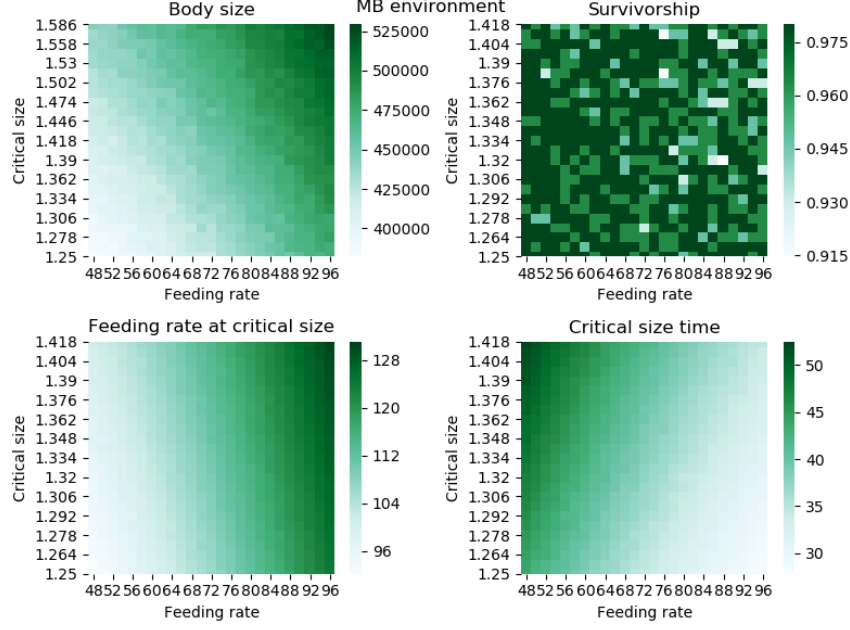


Figure 3.4: Effect of initial feeding rate and critical size on larval traits in MB culture

## 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 survivorship at MCU density. Lower critical size shows trend for higher survivorship, since larvae are able to pupate in lesser time before food quality decreases drastically.



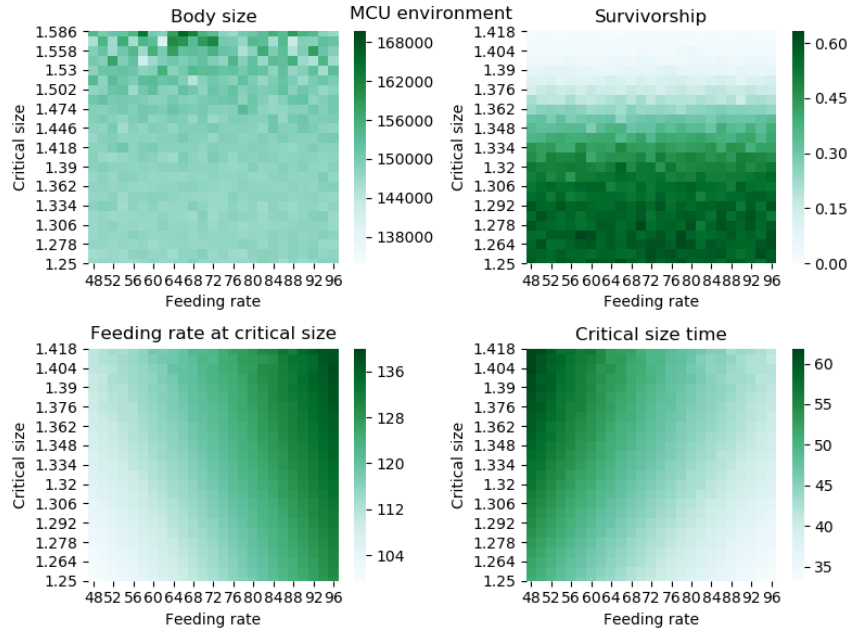


Figure 3.5: Effect of initial feeding rate and critical size on larval traits in MCU culture

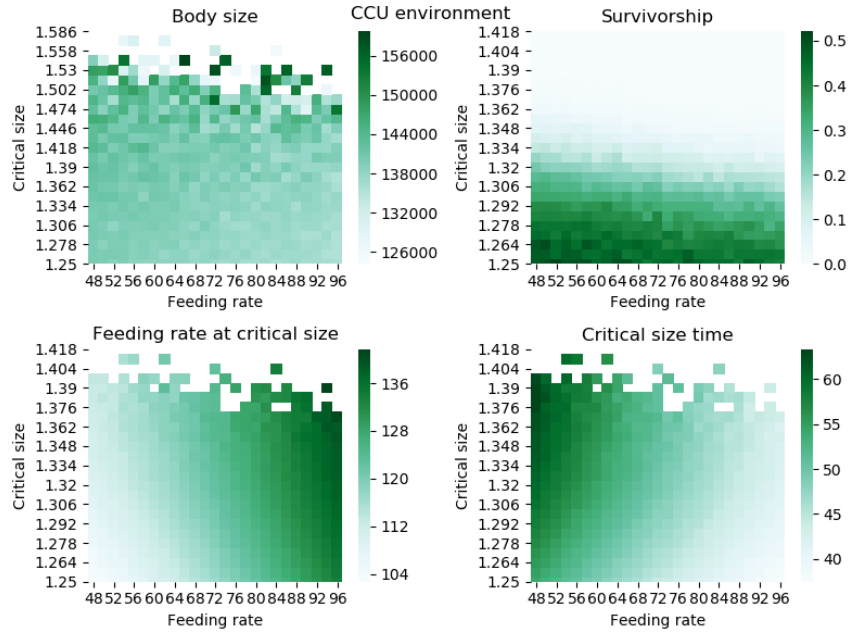


Figure 3.6: Effect of initial feeding rate and critical size on larval traits in CCU culture

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 leads to decrease in critical size thus feeding rate shown at critical size reaches lesser maxima. Survivorship shows no effect of these parameters at low density.

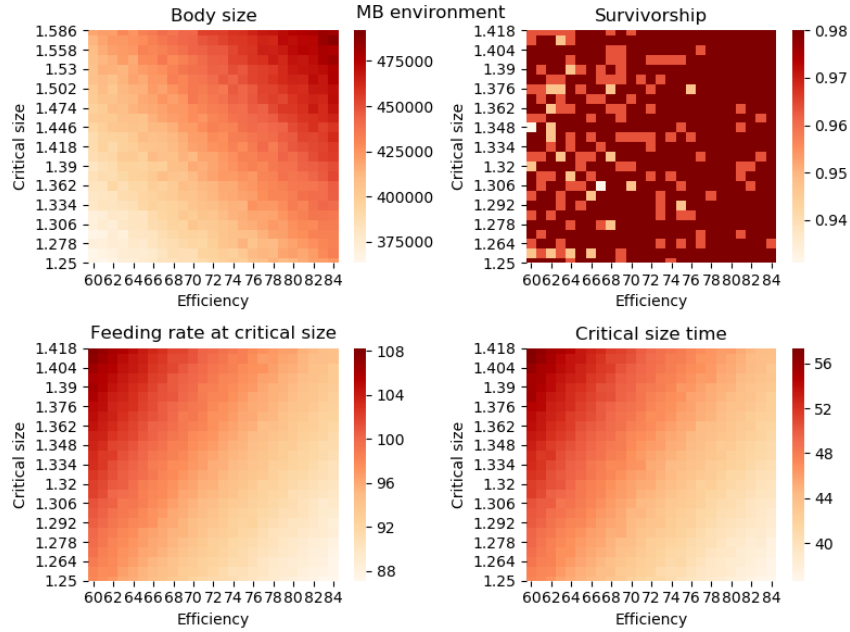


Figure 3.7: Effect of critical size and efficiency on larval traits in MB culture

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 survivorship maxima are lesser at high density.

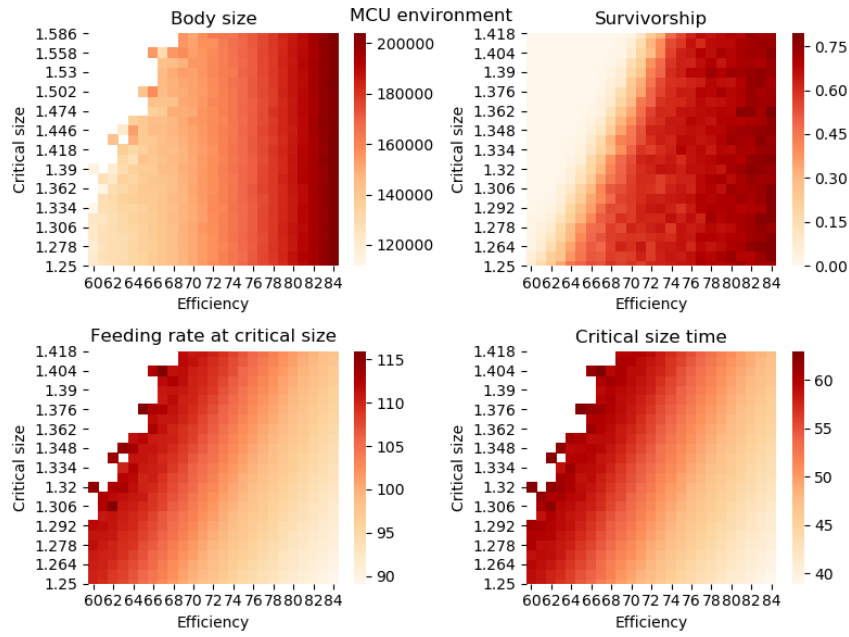


Figure 3.8: Effect of critical size and efficiency on larval traits in MCU culture

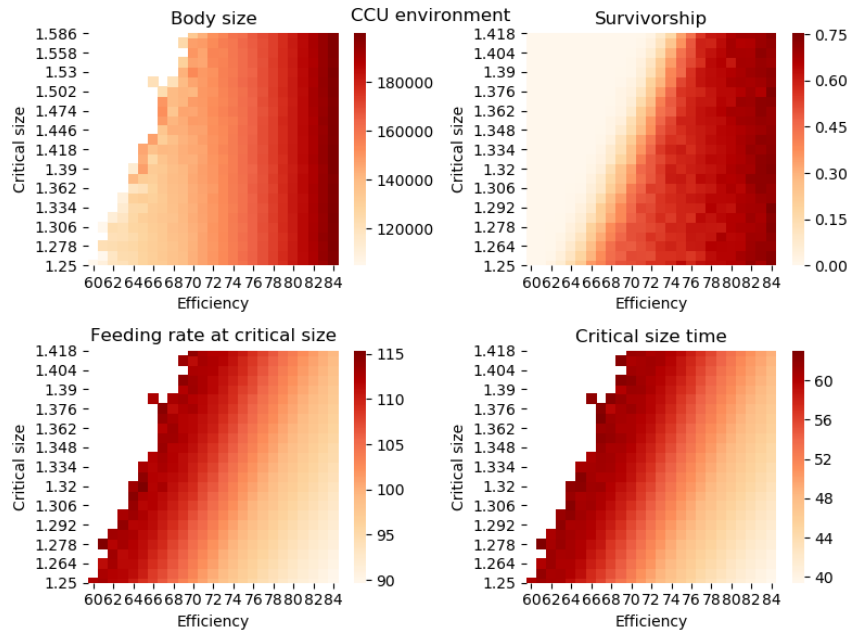


Figure 3.9: Effect of critical size and efficiency on larval traits in CCU culture

## 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, 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 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 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

$\delta_T$  = Stochasticity in mid-parent value of the trait  $T$

$N(mpv, \delta)$  = Normal distribution with  $mpv$  as mean and  $\delta$  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 initial 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).

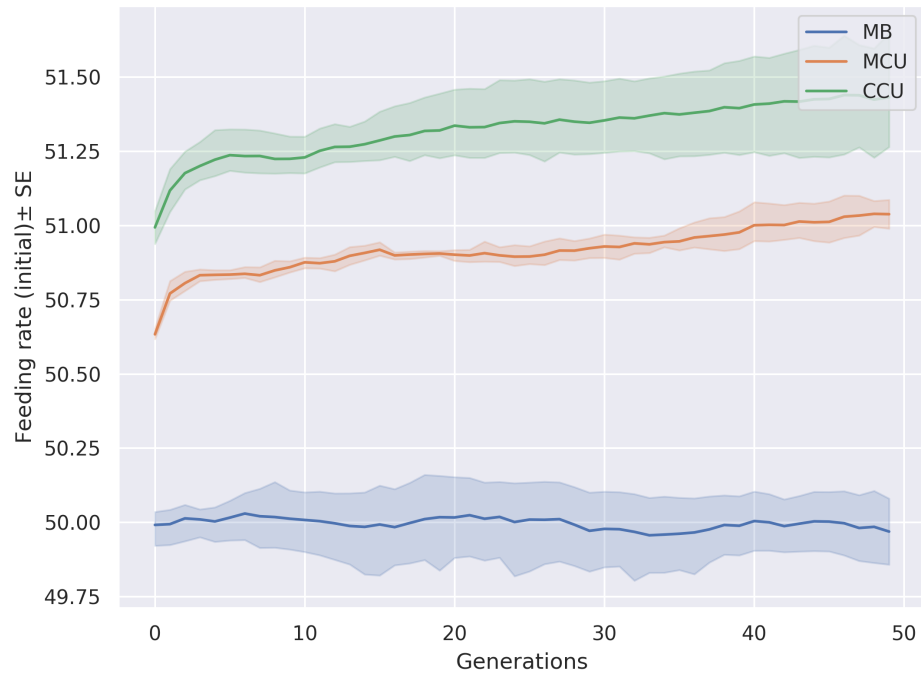


Figure 4.1: Timeseries for initial feeding rate

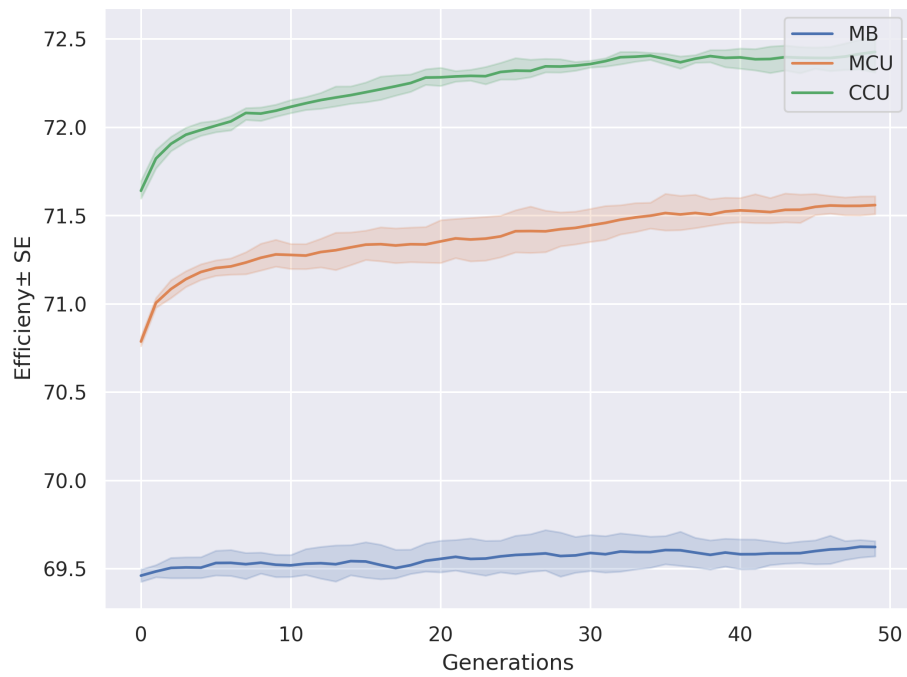


Figure 4.2: Timeseries for initial efficiency

## **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 heritability 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 achieve 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 such as body size, time to reach critical size and survivorship.

### **4.3.2 Heritability in Mid-parent Value**

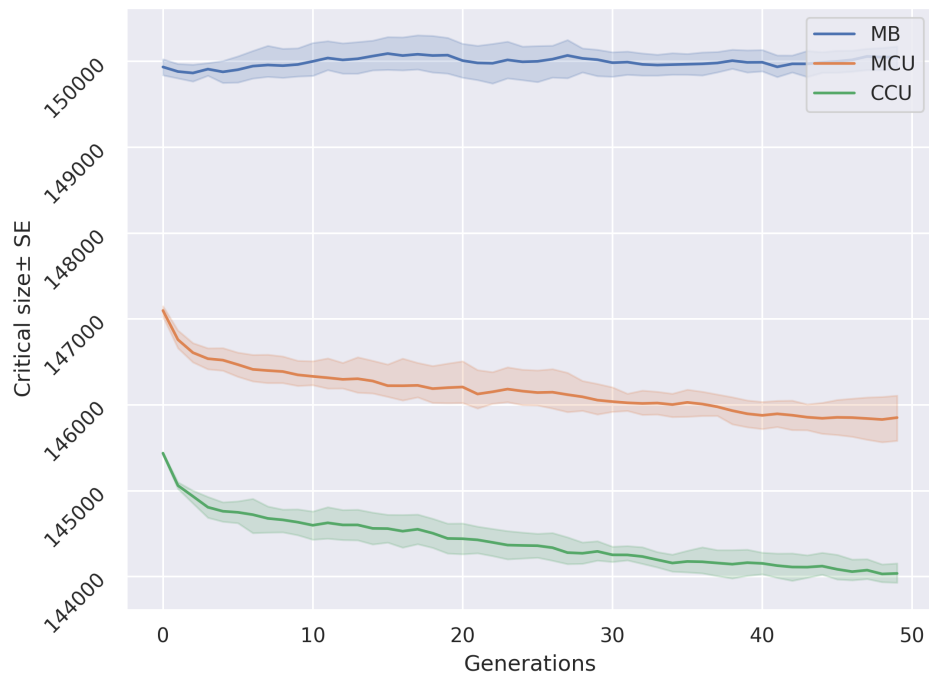


Figure 4.3: Timeseries for initial critical size

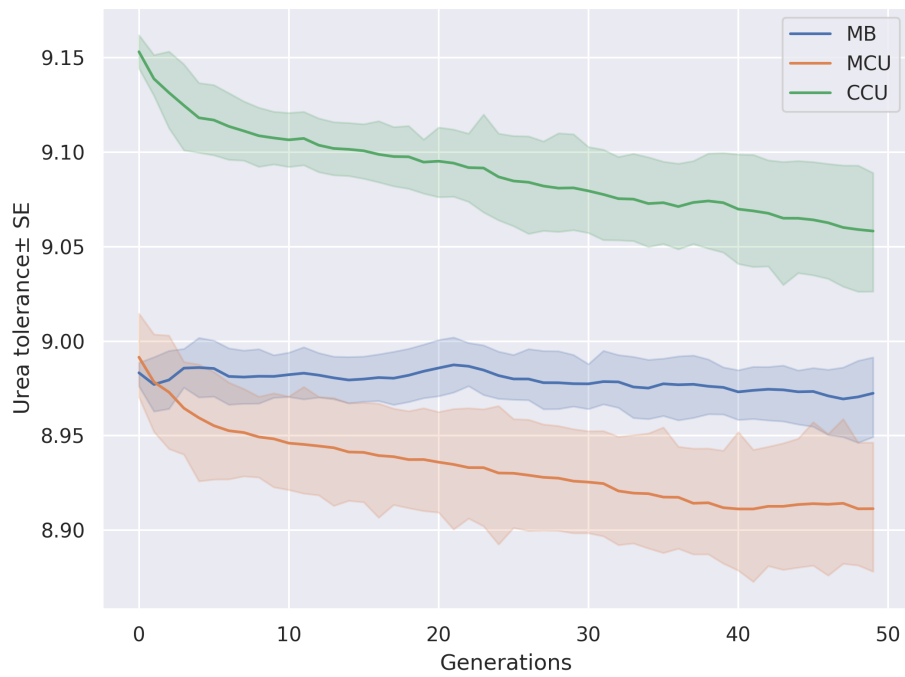


Figure 4.4: Timeseries for initial waste tolerance

# References

## Chapter 5

# Introducing Correlations in Larval Trait Parameters

### 5.1 Distribution of Laral Traits with Development Time

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

### 5.3 Discussion

# References

# Appendix A

## Chapter Title

### A.1 First Section Title

[1-2][?]

#### A.1.1 First Subsection Title

[3]

### A.2 First Section Title

[4-5]



# References