

**Adaptive Dynamics for an Age-structured population model with a
Shepherd recruitment function**

Michelle Heidi Ellis

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University of the Free State

Bloemfontein 9300

South Africa

Moderator : Prof. S.W. Schoombie

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Contents

1	The Evolution of ..	7
1.1	Evolution	8
1.2	A Suitable Density Mechanism	10
1.2.1	DDM's without density rate parameter	13
1.2.2	DDM's with density rate parameter	16
1.2.3	Parameter interpretations	20
1.3	Game Theory	22
1.4	Moving Forwards From Chapter 1	26
2	A Well Defined Evolutionary Game	27
2.1	EGT and the ESS Game structure	27
2.1.1	Different EStS scenarios	31
2.2	Adaptive Dynamics and the Rules of the ESS Game	32
2.2.1	Frequency Selection	32
2.2.2	Strategy selection	33
2.3	The Competition Model	34
2.3.1	The resident	35
2.3.2	The challenger	38
2.3.3	The combination	40
2.3.4	The fundamental theorem of natural selection	41
2.4	The ESS Criteria	44
2.5	Summary of Acronyms and Terminology	45
3	The Age-Structured Model	49
3.1	The Shepherd Recruitment Function	49
3.1.1	Defining age-structure	50
3.1.2	Including density	51
3.2	Periodic Point Analysis	53
3.2.1	Is a fixed point solution possible?	54
3.2.2	Model parameters conducive to a period two solution	55

3.2.3	Model parameters conducive to a period three solution	58
3.3	Quasi periodic Solutions	65
3.4	Useful results from Chapter 3	67
4	The Optimizing Algorithm	69
4.1	The Search Algorithm	70
4.2	The Gradient Search Program	71
4.2.1	Algorithm alternatives and short cuts	76
4.3	Algorithm Points Worth Remembering	78
5	The Gallery	81
5.1	Preliminary Discussions	81
5.2	Algorithm Outcomes	85
5.3	Visual Representations	85
5.3.1	Discussions from the gallery	86
5.4	The Pacific Sardine Population	95
6	The Stage-Structured Model	101
6.1	Defining Stage-Structure	101
6.1.1	Setting the stage	101
6.1.2	Determining the values of P and Q	103
6.2	The Kudu Population	105
6.3	On The Stage	107
7	In Conclusion	109
A	Period Three and Chaos	113
B	The Stage-Structured Algorithm	117

PREFACE

“Adaptive dynamics for an age-structured population model with a Shepherd recruitment function”, is about re-assigning the Shepherd density driven function to act as the recruitment function of an age-structured population model as apposed to its use as a growth rate function in the non age-structured case. It is also about applying adaptive dynamics to the model as apposed to game theory when predicting evolutionary outcomes.

Bellows found that the non age-structured model

$$X(n) = \frac{r}{1 + \left(\frac{X(n-1)}{\mathcal{K}}\right)^u} X(n-1) \quad u > 1, \quad (1)$$

for different values of the parameter u , best fit 19 of the 30 sets of data collected from insect populations showing density intelligence [11]. J.G. Shepherd, after whom the Shepherd model was named, introduced the model into the fishing industry in 1982 relating $X(n)$ to spawning stock biomass, r to the maximum expected rate of recruits per adult and \mathcal{K} to the biomass level above which density curbing with (strategy) strength u will occur [91].

Getz [52] and Getz and Schoombie [105] saw the parameter u as representing an evolutionary strategy, and investigated the evolutionary dynamics of u in (1). It was termed the ‘abruptness’ parameter by Getz as it controls the rate at which density dependence sets in around \mathcal{K} . The value of u was then calculated from a game theory perspective where the invasion immunity of the resident population was turned into a finite series of (few and far between) games between a resident populations and a population operating at a slightly different abruptness level, but otherwise indifferent. Evolution happens every time the resident is replaced by the competing population and is terminated when invasion no longer occurs. The term “evolutionary stable strategy” or ESS was used to describe the strategy u that rendered the population immune against any further invasion. It was found that r , usually between 1 and 2, controlled the behavior of the model, generating complex behavior at the lower limit and ordinary periodic behavior as r increases to the upper limit. The winning strategy values ranged from larger values at chaotic behavior to smaller values as the behavior became more predictable. In fact, they found that the relationship between u and r was given by

$$u > \frac{2r}{r-1} \quad (2)$$

The biological interpretation of their findings were associated with the dispersal mechanism adopted by the females of the specie with the possible intent to keep population numbers stable [52].

The purpose of this study is firstly to better define the differences between the ESS, the convergent stable strategy and the neighborhood invader strategy, secondly to decide where to incorporate the density function in an age-structured population model, thirdly to address the question of the existence of an ESS in the age-structured case by making use of a combination of adaptive dynamics and game theory and lastly to link the ESS to a population's strategy evolution potential. A very useful algorithm and periodic predictors are two of the useful outcomes of this study.

"Please, Mr. Gandolf, sir, don't hurt me. Don't turn me into anything..unnatural."
- Lord of the Rings, J.R.R. Tolkien

Chapter 1

The Evolution of ..

Since the dawn of ecology around 610 BC naturalists and philosophers have been debating the underlying mechanisms responsible for the many unexplainable observations in ecology. Previous debates on this matter ranged from the super natural to the naturally super such as Darwin's natural selection, Mendelian genetics, Maynard Smith's evolutionary game theory (EGT) and Metz *et al's* adaptive dynamics (AD) [16, 36, 3, 48, 64, 65]. The contribution of these four supers and many others have been priceless in seeking explanations to the mysteries of reproductive success of variants within an ecological population; specifically for those who can strategize for a best fit amidst environmental limitations. Their motivation was that a population capable of strategy adaptive dynamics, either through learning and therefore evolving or a random mutation¹ followed by natural selection² will be better equipped for successful reproduction [106].

But how?

1. Chapter 1 is dedicated to the attempts made by the fathers of evolutionary thinking in answering this question. The term 'strategy' will refer to the characteristic, trait or plan of action implemented by a population that gives them the ability to regulate their reproductive rate, but it can actually refer to any survival tool implemented by a population [121, 75, 76]. The mathematical operators designed to simulate the implicit behavior within a population will be investigated followed by an overview of game theory which was used to simulate their explicit behavior.
2. Chapter 2 is dedicated to the rules of a well defined evolutionary game. One that will evolve the 'perfect' population.

¹Genetic variations where a gene changes slightly resulting in trait change that will or will not be favored by the habitat

²When the Environment favors a strategy above other strategies.

3. Chapter 3 formulates the age-structured population model, incorporating the density mechanism of choice as discussed in Chapter 1 and implementing the rules of Chapter 2.
4. Chapter 4 describes the secrets of the strategy optimizing algorithm formulated by the interaction between age structure, adaptive dynamics and the Shepherd recruitment function.
5. Chapter 5 is the gallery where the outcomes of the algorithm are discussed with regards to the hypothetical data sets and actual data from the Pacific sardine population.
6. Chapter 6 formulates the stage-structured population model with a density mechanism. A slightly adjusted version of the age-structured algorithm is then applied to the stage-structured Kudu population in the Kruger National Park.
7. Chapter 7 evaluates the success of the research described in this work.

1.1 Evolution

In ancient times, myths, legends and religion were used to explain phenomena man had no control over [62]. The first recorded evidence of man seeking logical explanations for some of these phenomena reaches as far back as 610 BC in the ancient Greek, Roman, Chinese and Islamic cultures. In the field of ecology, ancients compared living species to fossils and based their theories on these observations. They saw similarities between species and speculated over the forming of new species and diversity of traits within a species. It was soon evident that the earth was much older than they thought. They wanted to know why some species shared common organs; was it common use or common ancestry? The other point of ponder was that if they did all share a common ancestry, then what caused the diversity? A popular solution was based on creation, that species carried an inherent pre defined mechanism to change. It was only in 1859 when Charles Darwin published his evolutionary theory in *On the Origin of Species* that natural selection provided an explanation for evolution³ that did not borrow from the super natural [32]. Darwin postulated:

1. Natural selection: individuals within species vary and some of these variations are heritable leading to descent with modification.

³The long term consequences of small changes in a population's genetic pool [15].

2. Darwinian fitness: individuals vary in their ability to survive and reproduce in a particular environment.

3. Adaptation: individuals with the most favorable adaptations, that is, a trait that will increase the fitness of an individual, are more likely to survive and reproduce.

Herbert Spencer coined the phrase ‘Survival of the fittest’ as an alternative expression for the above where ‘fit’⁴ does not refer to a physical trait, but instead to the probability that the species will survive long enough to reproduce [109, 84]. Darwin could however not explain the mechanism responsible for the variation in traits and how it propagated to the next generation and eventually evolve into a new species. This led to the ‘eclipse of Darwinism’ in the period 1880 till 1920. The opposition at that time argued that mutations could be a possible driving force behind evolution but this was disproved between 1910 and 1915 by T.H. Morgan who proved through experimentation that mutations were only responsible for diversity in a species and not so much in the establishment of a new species. In 1900 Gregor Mendel’s laws of inheritance were rediscovered by amongst others, Hugo de Vries who coined the term mutation, William Bateson who coined the term genetics and Carl Correns. Mendel discovered that there was a pattern in the propagation of certain discrete traits in pea plants and that there are dominant and recessive traits. He explained that offspring only inherit specific trait factors, later known as genes, from their parents leaving the population with plenty of variation. Mendelian genetics became the study of inheritance of discrete characteristics and was opposed by those who viewed inheritance as a more continuous blending (averaging) process which was also unfounded as continuous blending would lead to a population without varying traits. Universal acceptance of Darwin’s theories were only made possible and integratable with other biological fields when Sir Ronald Aylmer Fisher boldly stated in his book *The Genetic theory of Natural Selection* that the inheritance of many discrete characteristics could add up to an eventual continuous blending of characteristics and, if followed by natural selection, could evolve into a new species in the long run [47]. Most of Darwin’s ideas were anticipated by great thinkers reaching back as far as the ancients but what makes Darwin’s ascent memorable was that he conceptualized the ideas at the right time. Some of the main contributors to evolutionary thought are listed in Tables 1.1, 1.2 and 1.3.

⁴Fisher was the first to use ‘fit’ as an alternative to previous descriptions such as ‘selective advantage’ [84]

EVOLUTIONARY TIMELINE [610 BC- 1798]

Date	Observations
610 BC	Anaximander of Miletus: Speculated from the existence of fossils that all animals originated from the sea [63].
495 BC	Empedocles of Acragas: Humanity first comprised of complex structures that with time disappeared except for a few rare cases where the complex ingredients were compatible, a fore runner of Darwin's theory of natural selection. [19]
384 BC	Aristotle: He classified organisms according to their complexity and believed that all organisms were created for a divine purpose [112].
354 BC	Saint Augustine: God created the world in a single moment and then gave it the ability to develop [79].
<i>No further development was recorded after this period until the eighteenth century.</i>	
1735	Carl Linnaeus: Father of Taxonomy and author of <i>System Naturae</i> initially believed that species were unchangeable but through his observations later on in his life changed this view to new species arising from the beginning of creation through hybridization, a crossing between individuals belonging to separate populations which have different adaptive norms. [54]
1749	Georges-Louis Leclerc Buffon: He published his 44 volume encyclopedia <i>History Naturelle</i> where he debated the similarities between apes and humans and suggested a common origin shaped by an internal predefined mechanism [54]
1798	Thomas Malthus: He wrote in his <i>Assay on the Principles of Population</i> that overproduction of young and the inability of the habitat to provide more resources will result in competition amongst the siblings. Some of these siblings will have an advantage over others therefore giving rise to a superior population [54].

Table 1.1: Timeline of observations leading to evolutionary thought [610 BC - 1798]

1.2 A Suitable Density Mechanism

Naturalists, experimentalists and mathematicians all agree that successful populations have the ability to regulate their densities [97]. Initial growth in the absence of competition might be rapid but as soon as the carrying capacity of the ergodic⁵ environment is in jeopardy, competition for resources, predation and risk of disease will result in a reduction in the population's growth rate. This is a survival mechanism, ensuring a balanced habitat-specie relationship. Without such a mechanism, populations would grow limitlessly depleting all resources and lead to eventual population extinction. A suitable model should address such environmental issues as well as fit observed data patterns and address underlying theoretical reasonings on processes of interest. Some of the factors that can be considered when moulding a population model are listed below:

⁵Environment fluctuates but with no permanent effect [84, 82].

EVOLUTIONARY TIMELINE [1802-1829]

Date	Observations
1802	Erasmus Darwin: (Darwin's grandfather) wrote in his poem <i>The Temple of Nature</i> "...as successive generations bloom, New powers acquire and larger limbs assume.". He observed animal behavior and concluded that competition and sexual selection could bring forth changes in a species [54]
1809	Jean-Baptiste Lamarck: First stated possibility of evolution. first law in his book <i>Philosophie Zoologique</i> : Use or disuse of a certain characteristic of a specie can cause the characteristic to either enlarge or shrink. Second law: These changes are heritable. Lamarckian evolution provided a mechanism for understanding heredity. Successive hereditary of better characteristics would eventually evolve into a perfect specie. [54]
1813	William Charles Wells: The first recognition of natural selection. He observed that immunity and skin colour of man fits the country he inhabits [32]
1818	Etienne Geoffroy St. Hilaire: His book <i>Philosophie Anatomique</i> he saw all vertebrates sharing common organs as modifications of a single form which lead to the following response by George Cuvier:
1829	Georges Cuvier: If there are resemblances between the different forms it is only that they share similar functions and are not from a common origin. He ascribed population progression to bouts of extinction followed by re-creation which was evident from fossils of species that no longer exist. He also classified animals into four branches namely Vertebrata, Insecta, Vermes and Radiata [54].

Table 1.2: Timeline of observations leading to evolutionary thought [1802 - 1829]

1. Models can be made to be deterministic where no randomness is involved in the defining parameters, ensuring the same outcome for a given set of initial conditions. It will be seen in this study that it is however possible for a non linear deterministic system to evolve to a quasi periodic or chaotic state where using the same set of initial conditions can produce an outcome that seems different every time but is part of a regular pattern.
2. On the other hand, models can be made to be stochastic to suit an ever changing environment where data is approximated statistically from previous collected data [50, 33]. It adds a certain amount of randomness to the outcome even when using the same set of initial conditions. In ecology the carrying capacity⁶, shown as \mathcal{K} , of the environment as well as the birth and mortality rates of a population are usually stochastic. Evidence of this can be seen in, for example, the Kruger National Park where the amount of rain will change the vegetation which in turn will affect \mathcal{K} for the Kudu population, the temperature of the sea water will have an effect on the birth rate of the Pacific sardine population and

⁶ \mathcal{K} represents the maximum density the environment can carry without exploitation.

EVOLUTIONARY TIMELINE [1830 - 1851]

Date	Observations
1830	Charles Lyell: He published his book <i>Principles of Geology</i> that argued that the present holds the key to the past, that an accumulation of small changes over a very long time gave rise to geological change [54].
1831	Patrick Matthew: First inclination towards natural selection was in his book <i>On Naval Timber and Arboriculture</i> in where he suggested that trees with lesser strength will be replaced by the more perfect of their own kind, a form of natural selection that favors the stronger tree [125].
1843	Richard Owen: Defined the word <i>Homology</i> as “the same organ in different animals under every variety of form and function” after noticing that a bat’s wing, a cats paw and a human’s hand were all variants of the same form due to its use but not as a result of a common origin [54].
1851	Louis Agassiz: <i>Essay on Classification</i> where he compared fossils at lower levels in rocks to those higher and ascribed the differences to the Divine Plan of God [54].

Table 1.3: Timeline of observations leading to evolutionary thought [1830 - 1851]

the temperature of the ground will again influence the length of the pupae stage of the Tsetse fly which will have an effect on their mortality rates [95, 91, 26]. In this study, the parameters representing the carrying capacity, mortality and birth rates will be averaged and taken as constants to keep the complications to a minimum as the incorporation of age structure and density dependence into a population model already provides enough complicated entertainment. With the application of the model to real world situations in Chapters 5 and 6, however, some modifications will be made to accommodate certain periodic characteristics.

- Processes can be modeled with differential equations, relating the rate of change in a population’s density to its current density

$$\frac{dX}{dt} = \mathcal{R}(t)(X(t)) \quad (1.1)$$

Where \mathcal{R} expresses the specie- specific relationship, its sign and size indicating the extent of the growth or decay.

- Alternatively, the growth of a population can be modeled discretely using the difference equation

$$X(n + 1) = \mathcal{R}(n)X(n) \quad (1.2)$$

Where \mathcal{R} represents the per capita growth rate from one generation to the next.

5. They can be made to be density dependent models (DDM's). The density X of a population living in an environment E is very reliant, amongst other influences, on the carrying capacity \mathcal{K} associated with this environment [82, 84]. To keep population densities within the boundaries of \mathcal{K} , DDM's can be formulated to include a density feedback loop (a mechanism that curbs over population) that will accelerate growth rates at low densities and decelerate growth rates as densities reach or exceed \mathcal{K} . This loop keeps the population density in a neighborhood of \mathcal{K} , usually associated with densities exhibiting either asymptotic or oscillatory behavior around \mathcal{K} , but more on this later [5]. Another very important parameter that can be included in the design of a DDM, is the rate u at which the growth rate should accelerate/decelerate as population densities increase.

A few popular DDM's used in ecology for modeling insect and fish populations will be discussed next [71, 72, 86, 50, 108]. They will be divided into two groups, those with a density sensitive parameter u and those without.

1.2.1 DDM's without density rate parameter

1. The Exponential Growth Model

In 1798 Thomas Malthus wrote in his *An essay on the principle of population* that without intervention certain populations can increase at a rate proportionate to the population's current numbers [68]. This rate of change in population growth is the result of the difference between new entries (births, not immigration) and those that exit the dynamics (deaths, not emigration). That is, for a population in a constant environment with a constant birth rate b and death rate d , the rate of change can be expressed as the continuous Malthusian exponential growth model

$$\frac{dX(t)}{dt} = (b - d)X(t) = r_M X(t) \quad (1.3)$$

$$\text{where } r_M = b - d \quad (1.4)$$

r_M is referred to as the 'intrinsic rate of natural increase' or the Malthusian parameter and represents the rate of increase (if positive) or decrease (if negative) of the population [84]. Since r_M is a constant, the solution to (1.3), if the initial population size is X_I , is given by

$$X(t) = X_I e^{r_M t} \quad (1.5)$$

This means that in an unchallenged environment, X will either become extinct or grow exponentially depending on the sign of r_M . Joel E Cohen, author of *How*

many people can Earth support, stated that there is practically no evidence of a population growing limitlessly and that the exponential growth model, although useful, can only be used for short term population predictions (for instance during the acceleration stage mentioned earlier) [60]. Converting the continuous Malthusian exponential growth model into a difference model requires substituting $X(t)$ with its discrete version $X(n)$ and the derivative with the difference formula:

$$\frac{dX}{dt} \approx \frac{X(n+h) - X(n)}{h} \quad (1.6)$$

where $h = 1$ as $n = 1, 2, ..$ are the discrete time intervals at which X will be calculated.

$$\begin{aligned} X(n+1) &= (1 + r_M)X(n) = \mathcal{R}_M X(n) \\ \text{with solution: } X(n) &= X_I (\mathcal{R}_M)^n \end{aligned} \quad (1.7)$$

2. The Logistic Growth Model

The Malthusian growth model inspired P.F. Verhulst to publish his logistic model in 1838. He proposed that, when population densities become too large, a curbing mechanism should be activated [88]. His work was rediscovered by Pearl & Reed in 1920 and the logistic equation is therefore also referred to as the Verhulst-Pearl equation [52, 96]. Verhulst was interested in the logistic growth function as it exhibited an S - shaped (sigmoidal) behavior similar to the S- shaped data curves associated with certain ecological populations. These populations exhibit initial exponential growth followed by a deceleration process once some ceiling or saturation value has been reached as opposed to limitless growth as predicted by the Malthusian growth model. The reasoning behind the logistic model is that the birth rate should decline and the death rate should increase once the ceiling value has been reached and then stabilize to maintain a healthy balance. What the Malthusian growth model lacked was natural control by ways of a density mechanism with a damping factor k_b for the birth rate and boosting factor k_d for the death rate, that is,

$$b = b_0 - k_b X(t) \quad (1.8)$$

$$d = d_0 - k_d X(t) \quad (1.9)$$

Where b_0 and d_0 are the initial birth and death rates of the population. If a population reaches an equilibrium state ($b = d$) at time t , then the population size $X(t) = \mathcal{K}$ represents the carrying capacity of the habitat. Equating (1.8)

and (1.9) and setting $r = b_0 - d_0$ (not to be confused with r_M) gives

$$\begin{aligned}\mathcal{K} &= \frac{b_0 - d_0}{k_b - k_d} = \frac{r}{k_b - k_d} \\ \text{or } k_b - k_d &= \frac{r}{\mathcal{K}}\end{aligned}$$

An alternative (density dependent) representation for (1.4) is then:

$$\begin{aligned}r_M(t) &= b - d \\ &= b_0 - d_0 - (k_b - k_d)X(t) \\ &= r \left(1 - \frac{X(t)}{\mathcal{K}}\right)\end{aligned}\tag{1.10}$$

the population growth model (1.3) now takes on the more controlled form

$$\frac{dX}{dt} = r \left(1 - \frac{X(t)}{\mathcal{K}}\right) X(t)\tag{1.11}$$

$$= \mathcal{R}_L(t) X(t)\tag{1.12}$$

$$\text{where } \mathcal{R}_L(t) = r \left(1 - \frac{X(t)}{\mathcal{K}}\right)\tag{1.13}$$

This is the well known continuous logistic model, which, when solved, leads to the sigmoidal logistic growth curve [88]:

$$X(t) = \frac{X_I \mathcal{K} e^{rt}}{\mathcal{K} + X_I (e^{rt} - 1)}\tag{1.14}$$

Whether the initial population density is more or less than \mathcal{K} , the population will eventually stabilize on \mathcal{K} as t goes to infinity. Since \mathcal{R}_L can take on negative as well as positive values, oscillatory behavior can be expected. When a discrete model is more appropriate, $X(t)$ can be replaced by $X(n)$ in (1.8) and (1.9) to yield the discrete logistic model:

$$X(n+1) = \left(1 + r \left(1 - \frac{X(n)}{\mathcal{K}}\right)\right) X(n)\tag{1.15}$$

$$= \mathcal{R}_L(n) X(n)\tag{1.16}$$

$$\text{where } \mathcal{R}_L(n) = \left(1 + r \left(1 - \frac{X(n)}{\mathcal{K}}\right)\right)\tag{1.17}$$

The rest of the DDM's will be presented as difference equations on account of their applications.

3. The Ricker model

In 1954 Bill Ricker suggested that the population growth model for the salmon population should be an exponential function that can show quick growth before saturation $b > d$ and a quick halt after $b < d$. The suggested model is very similar to the Logistic model except for the modification [100, 101, 102, 5]:

$$X(n+1) = e^{b-d}X(n) \quad (1.18)$$

$$= e^{r(1-\frac{X(n)}{\mathcal{K}})}X(n) \quad (1.19)$$

$$= \mathcal{R}_R(n)X(n) \quad (1.20)$$

$$\text{where } \mathcal{R}_R(n) = e^{r(1-\frac{X(n)}{\mathcal{K}})} \quad (1.21)$$

where the same density interpretation for $b-d$ was used as in (1.10). The growth rate will never be negative and the solution, be it an equilibrium, periodic or chaotic, is confined between two extreme values [88]. Figure 1.1(a) shows the behavior of the growth rate \mathcal{R}_R for the case $r = 1.8$ with $\mathcal{K} = 1$ and an initial population density of $X_I = 0.01$.

4. The Beverton-Holt model

Another model designed for use in the fishing industry was introduced in 1957 by Ray Beverton and Sidney Holt [13, 5]. They are best known for their book *On the dynamics of exploited fish populations* [13]. The oscillatory behavior of the logistics equation is rectified in this model by limiting the growth rate to positive values only which will lead to asymptotic behavior as X approaches \mathcal{K} as seen in Figure 1.1(b). The model suggested is:

$$X(n+1) = \frac{r}{1 + \frac{X(n)}{\mathcal{K}}}X(n) \quad (1.22)$$

$$= \mathcal{R}_{BH}(n)X(n) \quad (1.23)$$

$$\text{where } \mathcal{R}_{BH}(n) = \frac{r}{1 + \frac{X(n)}{\mathcal{K}}} \quad (1.24)$$

The population will initially increase at a rate proportional to r and then slow down as X approaches \mathcal{K} .

1.2.2 DDM's with density rate parameter

None of the above DDM's include a mechanism by which a population can adjust its 'fit' around \mathcal{K} . Their fate rests on X either being smaller or bigger than \mathcal{K} with no means of intervention or strategy evolution when competition for residency

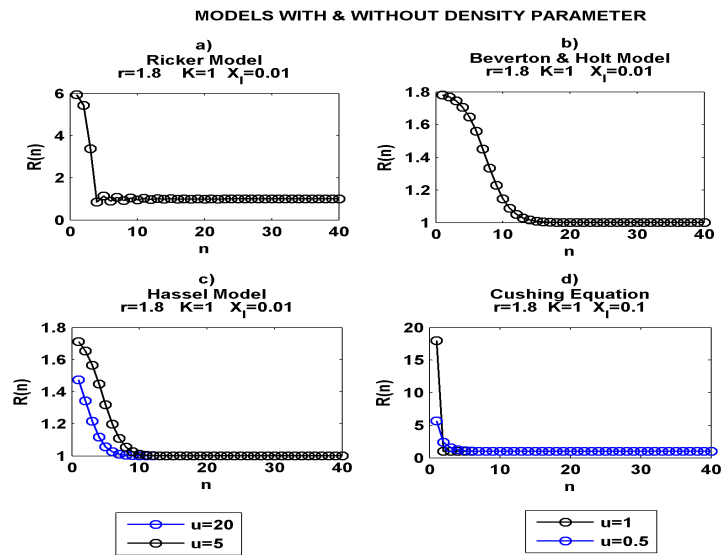


Figure 1.1: Figures (a) and (b) show the Ricker model and the Beverton-Holt model without a density rate parameter. Both these models converge to the carrying capacity of one. Figures (c) and (d) are respectively the Hassel and the Cushing models. Adjusting their density rates changes the speed of the convergence to the carrying capacity of one.

presents itself. To maintain or compete for poll position it might be necessary to keep population densities optimal which might require a tighter fit around \mathcal{K} or it might require a faster or slower convergence towards \mathcal{K} . Models that have been designed to adapt strategy under the rule of \mathcal{K} are the Hassel, Cushing and the Shepherd

(Beverton-Holt sigmoidal) models. They allow for this kind of intervention with the ‘best density fit under the rule of \mathcal{K} ’ parameter u . From this point forwards, u will be a scalar valued parameter and referred to as the strategy parameter.

1. The Hassel model

Hassel’s model (1958) is an alternative to the logistics growth model and the Ricker model and is used in the modeling of insect populations[60]:

$$X(n+1) = \frac{r}{\left(1 + \frac{X(n)}{\mathcal{K}}\right)^u} X(n) \quad (1.25)$$

$$= \mathcal{R}_H(n) X(n) \quad (1.26)$$

$$\text{where } \mathcal{R}_H(n) = \frac{r}{\left(1 + \frac{X(n)}{\mathcal{K}}\right)^u} \quad (1.27)$$

The top reflects the Malthusian growth model, showing exponential growth at low population numbers. With a population increase, the bottom part of \mathcal{R}_H will increase, slowing this exponential growth down [49]. It can be seen from Figure 1.1(c) that for $r = 1.8$, initial population density $X_i = 0.01$ and $\mathcal{K} = 1$, the larger u value shows faster convergence to \mathcal{K} .

2. The Cushing equation

In 1973 Cushing suggested the power form:

$$X(n+1) = \frac{r}{\left(\frac{X(n)}{\mathcal{K}}\right)^u} X(n) \quad (1.28)$$

$$= \mathcal{R}_C(n) X(n) \quad (1.29)$$

$$\text{where } \mathcal{R}_C(n) = \frac{r}{\left(\frac{X(n)}{\mathcal{K}}\right)^u} \quad (1.30)$$

For populations not evaluated at zero or near zero densities and $0 < u < 1$, this model will show a fast convergence to \mathcal{K} . The closer u is to 1, the faster the convergence and the larger the initial growth rate as seen in Figure 1.1(d) [111].

3. The Shepherd model

In 1982 Shepherd suggested a versatile three- parameter model which can mimic the Ricker model if $u > 1$, the Beverton-Holt model when $u = 1$ and the Cushing equation when $u < 1$ [111]. It will be the model of choice in this study due to its success in modeling certain insect and fish populations and is defined as [52]:

$$X(n+1) = \frac{r}{1 + \left(\frac{X(n)}{\mathcal{K}}\right)^u} X(n) = \mathcal{R}(n) X(n) \quad (1.31)$$

The best way to explain the dynamics of this model is with the aid of Figures 1.2(a) and 1.2(b) which shows the population growth function and density for different r and u combinations. The value of u can postpone the onset of density curbing by keeping the growth rate close to r for longer before settling down to values around \mathcal{K} , be it asymptotic or oscillatory. For a population with a fairly large initial growth rate of $r = 1.8$ as shown in Figure 1.2(a), the best fit around $\mathcal{K} = 1$ is for fairly small u values in comparison to the situation of Figure 1.2(b) where the smaller initial growth rate $r = 1.2$ requires larger u values to keep the growth rate closer to r for much longer with the purpose of extending optimal growth and delaying density curbing. A possible interpretation is that a populations initial growth rate will be large when there is an abundance in resources, but this comes with the risk of over populating the environment, the females will then encourage competition amongst the recruits by under dispersing them on resources, resulting in less surviving (and abruptly so) this exercise [52]. This under dispersal strategy is then associated with the smaller u value and vice versa for hard times associated with a smaller initial growth rate but larger u (over dispersing the young). For this reason, u is termed the strategy parameter or, for the Shepherd model specifically, the ‘abruptness’ parameter [52]. In Chapter 5 it will be shown that for the case $r = 1.8$, the strategy $u = 5.0499$ will result in the best fit around \mathcal{K} shown as the black plot in Figure 1.2(a). Values smaller than this will not stabilize the population on an optimal growth pattern as shown for $u = 2$ (the red plot in Figure 1.2(a)) where the females clump the young on resources to the extent that the survival rate is less than what is required for an optimal fit. Larger values such as $u = 10$ (the blue plot in Figure 1.2(a)) result in extreme highs and lows around \mathcal{K} , this is as a result of the females over dispersing their young and, with such a high growth rate, it will soon lead to population peeks followed by a sudden drop in population as resources are jeopardized. The extreme lows will make the population vulnerable to invasion by other strategists. If a population is evaluated on its ability to optimize densities under the rule of \mathcal{K} , that is, stay as close to \mathcal{K} as possible, then mathematically the optimizing should be done with respect to the strategy parameter u which controls the density spread around \mathcal{K} in the Shepherd model. The reasoning behind calculating an optimal strategy for a given r is that natural selection will favor this strategy in an environmental sense. From (1.31), the growth will be regarded as negative when $\mathcal{R} < 1$ and positive when $\mathcal{R} > 1$, that is, when:

$$\text{negative growth: } \left(\frac{X}{\mathcal{K}}\right)^u > r - 1 \quad (1.32)$$

$$\text{positive growth: } \left(\frac{X}{\mathcal{K}}\right)^u < r - 1 \quad (1.33)$$

Equations (1.32) and (1.33) also show the practical roll of r . If $u > 1$ and $r > 2$, there will be positive growth even when X exceeds \mathcal{K} . The growth rate will be slower but will only become negative once the upper buffer $\left(\frac{X}{\mathcal{K}}\right)^u = r - 1$ is reached and not necessarily at \mathcal{K} unless $r = 2$. Similarly the growth rate can become negative even before the population reaches \mathcal{K} if $r < 1$. Ideally, populations should be able to reach \mathcal{K} but not be allowed to exceed this value too drastically.

1.2.3 Parameter interpretations

Except for the Malthusian growth model, the above models have growth rates

$$\mathcal{R} = \mathcal{R}\left(\frac{X}{\mathcal{K}}\right) \quad (1.34)$$

which captures the density dependence as a decreasing function of $\frac{X}{\mathcal{K}}$. For the Beverton-Holt, Hassel and Shepherd models, a low population density $X \approx 0$ will show $\mathcal{R} \approx r$ which gives r the new interpretation as being the low density (but maximum) growth rate of the population, that is,

$$X(n+1) \approx rX(n), \quad X(n) \approx 0 \quad (1.35)$$

In the exponential growth model, $r = b_0 - d_0$, but it can also be seen as the proportion s of those born b that survive to the next time step or $r = bs$. Since a population will not survive if they do not immediately grow at low densities, it is a practical assumption that $r > 1$ as it must not only be able to replace itself but also add to the population total, that is, from (1.7)

$$r = 1 + r_M \quad (1.36)$$

where r_M is the proportion of $X(n)$ that will be added to the population total. Once the population has reached \mathcal{K} ,

$$X(n+1) \approx \frac{r}{2}X(n), \quad X(n) \approx \mathcal{K} \quad (1.37)$$

and the population growth should either remain constant here or fluctuate slightly around this value, therefore, r should not exceed 2 and ideally

$$|r_M| < 1 \quad (1.38)$$

The change in population dynamics when X approaches \mathcal{K} is ascribed to the competition between the members for resources where there is either a ‘scramble’ to be able to reproduce sufficiently or a ‘contest’ when only a few find enough while the others do not [92, 52]. There are other interpretations of the parameters r, \mathcal{K}, u and \mathcal{R} in ecology depending on the nature of the study, and they are listed below:

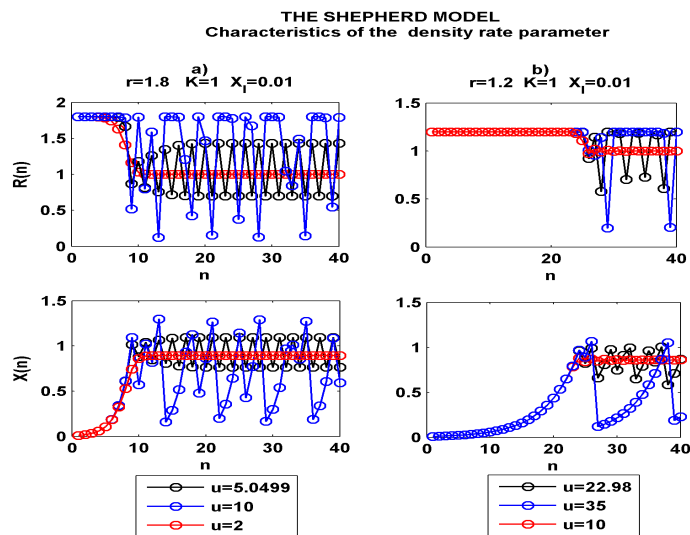


Figure 1.2: Figures (a) and (b) show the growth rates \mathcal{R} and the population $X(n)$ they generate for respectively $r = 1.8$ and $r = 1.2$. Three different u values were used to illustrate the effect this parameter has on the population fit around \mathcal{K} . If u is too small (red) the population will settle before reaching full potential, too high (blue), and the population can spike to extreme values, which can result in a spurge of both under and over population which might make the population vulnerable. The optimal value (black) will show a fine balance about \mathcal{K} .

1. r : ‘natural rate of increase’, ‘intrinsic growth rate’, ‘recruits-per-unit-biomass’, ‘proliferation rate’ or ‘maximum expected rate of recruitment’ [111, 91, 90].

2. \mathcal{K} : ‘carrying capacity’, ‘biomass level above which density dependence sets in’ or ‘threshold biomass’ [111, 91, 90].
3. u : ‘the rate at which the growth rate should adapt as population densities increase’, rate of ‘degree of compensation’, ‘measure of strength of density dependence’ or ‘abruptness parameter’ [52, 111, 91].
4. $\mathcal{R}(n)$: ‘growth rate’, ‘per capita growth rate’ or ‘fitness generating function’ [82, 109]. In a stage- or age-structured population formulation where the above models form part of the whole and they do not define the entire progress from $X(n)$ to $X(n + 1)$ themselves, the symbol $\psi(n)$ will be used to represent the density mechanism instead and $\mathcal{R}(n)$ which will be reserved for the expression linking $X(n)$ to $X(n + 1)$ where now

$$\mathcal{R}(n) = \mathcal{R}(\psi(n)) \tag{1.39}$$

The values of \mathcal{K} and u can be approximated by fitting the model best describing the population dynamics onto the data from the life tables. The u so found can then be compared to the optimal u^* calculated from the optimization algorithm in Chapter 4 and can then be used to establish the direction of future species evolution or allow human intervention for optimal harvesting without exploitation [50]. It will also be seen in Chapter 5 that r need not necessarily be constant but can be made time dependent to simulate certain types of population behavior such as periodic growth peaks.

1.3 Game Theory

A game evolves when there are players, strategies, game structure, pay-offs and rules. Classical game theory was introduced to mathematics in the 1940’s by John von Neumann and Oskar Morgenstern in their 1944 book *Theory of Games and Economic Behavior* [78]. With a background in economics their studies entailed games between two players where one’s winnings matched the other’s losses which gave rise to the phrase zero-sum games. In 1950 John Nash suggested a game where all the players play a no-regret game [89]. It is in essence a study of conflict and cooperation between players capable of making decisions when it comes to choosing strategies from some fixed set of possibilities. The game rules assign a consequence to every possible combination of competing strategies played by the player and his opponent and the players have knowledge of these consequences and make ‘rational’ or well thought through choices based on this. If the players reach a point where neither can benefit from a change in strategy then they have reached a Nash equilibrium [61][123]. This

game is fully defined as all the cards are on the table and the game is played only once. In simple terms, each individual strategy in a Nash equilibrium is the best choice each player can make for that game, playing with open cards [78].

Mathematically, if $P(A, B)$ is the pay-off for playing strategy A against strategy B , then the pair (A, A) will represent a Nash equilibrium in this two player game if

$$P(A, A) \geq P(B, A) \quad B \neq A$$

is true for both players where B can be a similar strategy to A but not a challenging one. Classical two player games usually involve discrete behavioral strategies simulating animal tactics such as ‘wait’, ‘hide’, ‘fight’ and ‘retaliate’. This makes it ideal to represent the pay-offs in a matrix and the Nash equilibrium in such a matrix representation is then defined as that entry which is simultaneously:

1. The minimum value in the row it is in; other values in that row can be the same but not less ...and at the same time ...
2. The maximum value in the column it is in; other values in that row can be the same but not more.

This entry defines a saddle point for the matrix [127].

The branching from classical game theory to EGT came about as a result of the following observations in ecology:

1. The application of classic game theory to evolution was pioneered by Bill Hamilton who extended the fitness-game to include several rounds. The game can, for instance, be a strategy challenge where the player (or its kin carrying the same gene of strategy) with the better strategy will go through to a next round, facing yet another opponent and this process can carry on until there are no more suitable contenders [56, 57, 17, 18, 119, 120].
2. In ecology the game can be between different communities and not just two players. Their strategies are also inclined to be continuous (as opposed to discrete) and can be based on physical traits such as body size, flowering time and reproduction (Hamilton’s study of sex ratios) [78, 57].
3. In 1930 Ronald Fisher made the observation in *The genetical theory of natural selection* that the sex ratio of some mammal species remain balanced even though most of the males never mate, which indicated that ecological population have the ability to strategize according to need and not choose a strategy from a pre-defined set [47].

4. In 1973 Maynard Smith published his own ideas together with the ideas of George Price in *Evolution and the Theory of Games* in which they suggested that, following Fisher and Hamilton, in ecological games, the players need not necessarily be rational. In fact, the only requirement is that they each have a strategy (usually not by choice but by genetics) and the evolution-game will be judged on how natural selection favors these strategies, awarding the winner the higher reproduction ability [123].

Hamilton's concept of an 'unbeatable' strategy in 1967 inspired Maynard Smith's definition of an evolutionary stable strategy or ESS in his 1972 article *Game Theory and the Evolution of Fighting* [74]. He refined the 'unbeatable' definition by requiring the strategy to be the overall profitable one in the presence of alternative strategies, and if adopted by the whole population, then no member using a different strategy can invade. This is also where evolution comes to a stand still provided the environment they are in remains constant [74, 84]. Mathematically, if $P(A, B)$ is the pay-off for playing strategy A against strategy B , then the pair (A, A) will represent an ESS in this two player game if

$$P(A, A) > P(B, A) \quad \forall B \neq A \quad (1.40)$$

which is a stricter condition than the Nash condition [59]. An ESS is also a Nash equilibrium but not necessarily vice versa. Some of the popular games of EGT are listed next showing the differences and similarities between the Nash equilibrium and the ESS:

1. Hawk/Dove: Probably the most classic game and Maynard Smith's starting point. It is a Contest over a shared resource P . In the same species contestants can play either Hawk (fighter) strategy or Dove (retaliate) strategy. It explains why some animals engage in ritual harmless fighting as opposed to fighting to the end. If C represents losses as a result of injury then the pay-off matrix representing the game is given by:

	meets Hawk	meets Dove
if Hawk	both win and loose: $\frac{P}{2} - \frac{C}{2}$	Hawk wins: P
if Dove	Dove loses: 0	Doves share: $\frac{P}{2}$

A member of the species whose strategy it is to first study the behavior of its opponent, and acts Hawk when the opponent is deemed weaker (usually smaller), and acts Dove when the opponent seems stronger is using an Assessor strategy and it will be an ESS [75].

2. The War of Attrition: A contestant high on resources but low on gaming skills attempts to win a game by wearing down the opponent through continuous loss of resources [76]. The contestants decide whether the non sharable pay-off P is worth their losses. After P comes into play, an auction follows and the highest bidder with bid V wins P . The catch is that both lose resources v equal to the lowest bidder's bid. Bidding higher than P seems irrational but remember that each bidder only pays the lowest bid. The only limit to the bidding is the player's resources. Possible outcomes are:

- (a) $(v < V) > P$: loser pays more for his loss but winner pays less and wins resource
- (b) $(v < V) < P$: winner wins resource but benefits by an amount $V - v$
- (c) $(v = V) < \frac{P}{2}$: both gain $\frac{P}{2} - v$
- (d) $(v = V) > \frac{P}{2}$: both loose $\frac{P}{2} - v$

No choice of bid will be beneficial in all cases not knowing the other's bid resulting in no dominant strategy for this game. If a player had knowledge of the others abilities and resources and decides to bid $v = 0$ (no winnings but also no losses) while the other bids $V > P$ it would represent a Nash equilibrium but not an ESS as there is no single V that will be best.

3. Prisoner's dilemma: Both players act in their own interest even though cooperation would have been mutually beneficial. Merrill Flood, Melvin Dresher and Albert W. Tucker formalized the game as follows: two prisoners A and B are questioned separately they are both offered the same deal either betraying (defect) each other or remaining silent (cooperate). The pay-off matrix shows the possibilities [100]:

	B silent	B betrays A
A silent	each serves 1 year	A 1 year, B free
A betrays B	A free, B 1 year	each serves 3 months

4. Iterated prisoners dilemma: If the two players repeat the above game with memory of previous games changing their strategy accordingly they will eventually reach a Nash equilibrium where both betray each other. This is also an ESS as it is the best combination of all [9, 100].

1.4 Moving Forwards From Chapter 1

The above mentioned EGT games all have well defined game plans and rules (re-defined in some cases) to lead to pay-offs either being a Nash or ESS equilibrium. In Chapter 2 an ESS pay-off game will be formulated for a finite set of games between the female members of the same population using dispersal strategies that differ only by a very small amount. Players using two different strategies will compete against each other with the player with the winning strategy becoming the resident. Winning implies that of the two competing reproduction strategies, the winner best fits the environment defined by \mathcal{K} . The resident will then go forwards to the next round against a next player with yet another reproduction strategy variation. This process continues until a strategy as defined by the ESS formulation is reached. The game structure will be provided by EGT and the rules will be formulated from this.

“Certainty of death, small chance of success - what are we waiting for?”
- Lord of the Rings, J.R.R. Tolkien

Chapter 2

A Well Defined Evolutionary Game

An evolutionary game evolves when the fitness of an individual, already subjected to habitat limitations, is challenged by both its own strategy and the strategies of others. From the EGT discussion on Chapter 1 it was seen that:

1. Evolutionary games do not generally add up to zero.
2. Strategies are usually not pre-determined.
3. A game usually lasts more than just one round.

Clearly evolutionary games need their own structures, rules and pay-off interpretations. By combining EGT and mathematics the visual observations made in Chapter 1 of the mechanics of natural selection can be made more tangible in this chapter [78]. In all that follows, it must however not be forgotten that genes are the building blocks of the inheritable strategies carried by the player and its kin, and that one could just as well have played the game of interacting genes or evolutionary population genetics but, then again, it is the strategy that determines the interaction between a species and its environment and natural selection favors the strategy [115, 78]. Therefore, evolutionary games and their equilibriums will be strategy based¹, bypassing their underlying genetic make up [1, 24, 48, 116, 84].

2.1 EGT and the ESS Game structure

Being the owner of an ESS strategy is merely the pay-off of a so far undefined game. It is in itself not game defining as it does not stipulate how the evolutionary game must be played. The game of strategy evolution needs structure and rules! A good

¹Referred to as quantitative genetics or meso - evolution

way to start is by asking the right question:

“What must a strategy do to be awarded the ESS pay-off ?”

The answer to this question lies in the next discussion on matters of consequence:

1. A matter of environment E :

From a population perspective, the environment includes all factors that can potentially influence a population’s own behavior, be it non living such as weather (abiotic) or living such as predators and densities (biotic) [85]. In this work the environment E as perceived by the population will be its population density X as this will influence the strategy the population is using. It will serve as a growth buffer and is our old friend \mathcal{K} .

2. A matter of fitness:

In population genetics, fitness is defined to be the likeliness of a species to survive till reproduction age² [84]. In evolutionary ecology (on account of more complex population structures), fitness is defined as the ‘hypothetical average rate of exponential growth, which results from the thought experiment in which a clone of the type under consideration grows in an ergodic environment’ [85]. In constant environments this is the growth rate parameter r_M (or Malthusian parameter) [84]. It is a function of two variables, namely the characteristic of the population under consideration (in this case u) and the environment E defined by X . Mathematically,

$$r_M = r_M(u | E) = r_M(u | X) \quad (2.1)$$

and is interpreted as the fitness of a population employing strategy u in an environment E defined by X [84, 85]. As the fitness parameter r_M can be replaced by any other parameter that exhibits the same fitness outcome, it will be necessary to adapt the ‘average rate of exponential growth’ in the differential equation case to the average rate of $\log(\mathcal{R}(n))$ in the difference equation case as it will show the same outcome for our investigations, namely positive for positive growth, negative for growth reduction and zero for constant growth. $\mathcal{R}(n)$ itself can also be used but then positive fitness will be associated with $\mathcal{R}(n) > 1$, negative fitness with $0 < \mathcal{R}(n) < 1$ and zero fitness when $\mathcal{R}(n) = 1$. Note that for the difference equation case, when dealing with periodic solutions, this will involve taking the average of the log’s of the $\mathcal{R}(n)$ ’s defining this period, that is, for a difference equation spanning $m + 1$ discrete time intervals and with period N :

$$r_M \approx \frac{\sum_{k=1}^N \log \mathcal{R}_k(u, \bar{X})}{N} \quad (2.2)$$

²Also known as age of maturity

$$\text{where } \bar{X} = [X(n), X(n-1), \dots, X(n-m)] \quad (2.3)$$

and is better known as the invasion exponent I of the population [105]:

$$I(u, \bar{X}) = \frac{\sum_{k=1}^N \log \mathcal{R}(n-k)}{N} \quad (2.4)$$

$$\text{where } \bar{X} = [X(n), X(n-1), \dots, X(n-m)] \quad (2.5)$$

3. A matter of confusion:

An evolutionary singular strategy or ESiS is the term used for defining a strategy that evolves a population to an equilibrium followed by a zero fitness in the absence of competition [84]. In all that follows, the strategies evolved will all primarily be ESiS strategies. Writing the previous definition of an ESS strategy as being an unbeatable strategy in terms of environment and fitness would make it one such that a resident population using an ESS strategy u_R , is one that dominates and defines an environment X_R where all other contenders (of the same type) using a slight variation of this strategy must have non positive fitness in the environment defined by X_R [85, 74]. The resident will have zero fitness ($\mathcal{R}=1$) before the next contender arrives, since it is at an equilibrium and unchallenged (ESiS). An unbeatable strategy u_R is therefore one that will evolve an optimal population density X_R where, for all other nearby contenders X_i using strategies u_i ,

$$\mathcal{R}(u_R | X_R) = 1 \quad \& \quad 1 \geq \mathcal{R}(u_i | X_R) \quad u_i \neq u_R \quad (2.6)$$

Before more necessary features are added to this early ESS formulation, this version will be referred to as an EStS and read as an evolutionary steady strategy [84]. The reason why this version cannot be called an evolutionary stable strategy is because the current definition only states that other strategies should have non positive fitnesses, which means that they can also be zero, sharing the fitness pay-off which makes the resident unstable. The ESS formulation must also address the matter of how such a strategy is come by, that is, where does natural selection fit in? The assumption can be made that as soon as a better³ strategy presents itself, natural selection will favor this strategy which will then replace the previous one, and so on until a strategy evolves upon which cannot be improved. Such a strategy is then an evolutionary attractor and this convergence process defines how the evolutionary game will be played. Two additional features therefore must be added to the EStS formulation, namely convergence and the exclusivity of the evolutionary attractor. If u_R is an exclusive attractor then evolution will drive slight perturbations in u_R back to u_R making a tie with another strategy impossible. These two features are formulated as follows [85]:

³Resulting in a positive fitness.

- (a) Convergence: If u_R is come by through a finite sequence of u_i 's generating environments X_i such that the fitness of the contesting population employing strategy u_{i+1} in an environment defined by X_i generated by the previous strategy u_i is positive:

$$\mathcal{R}(u_{i+1} | X_i) > 1 \tag{2.7}$$

then u_R is an evolutionary attractor. The u_i 's in the sequence (2.7) are referred to as convergent stable strategies (CSS), so named by Taylor and Christianson [27, 117]. The CSS must not be confused with the continuous stable strategy (also CSS) (by Eshel and Motro in 1981 [39]) or the evolutionary unbeatable strategy (EUS) [82]. These two strategies refer to the CSS process ending in an EStS. Subjecting the new resident X_R to any other $u_i \neq u_R$ will result in a negative fitness and since u_R was come by through a series of fitness increments, $\mathcal{R}(u_i, X_R)$ will be more negative the further away u_i is in the line up. Note that the convergence process can also end on a plateau of strategies, all capable of evolving populations with very little variance, turning natural selection into a game of musical chairs and will therefore not ensure the exclusivity of u_R .

- (b) Exclusivity: To make sure that, once the convergence process brings evolution to the neighborhood of u_R , that natural selection will favor this value above all others, making this strategy stable against perturbations leading to a shared fitness⁴, the possibility of a plateau of similar strategies must be ruled out. One way would be to require that u_R is still the better strategy even when X_R densities are very low, that is, it must offer a distinctly different population fit about \mathcal{K} in comparison to the populations evolved at strategies in the neighborhood of u_R . This can be formulated as follows [37]:

If u_R was come by through a finite sequence of u_i 's generating environments X_i and is such that exposing any of these X_i 's to u_R will show positive fitness only:

$$\mathcal{R}(u_R | X_i) > 1 \quad \forall X_i \neq X_R, \tag{2.8}$$

then u_R will also be exclusive and referred to as a neighborhood invasion strategy (NIS). [6, 8].

The question of what makes a strategy an ESS strategy can now be answered: A strategy that, besides being *steady* (EStS) was also come by through a finite

⁴Also known as evolutionary branching points (EBP)

series of *convergent* strategies (CSS), and is also the only strategy capable of achieving this *stable* state (NIS) will be awarded the evolutionary stable strategy (ESS) pay-off:

$$\text{finite CSS series} + \text{EStS} + \text{NIS} = \text{ESS} \quad (2.9)$$

The Evolutionary process will stop once the population has strategized up to a point where its strategy cannot be improved upon under current biotic and abiotic conditions [82]. This is actually the ESS pay-off.

2.1.1 Different EStS scenarios

Experimental outcomes have showed that there are other possible outcomes to the evolutionary game. The starting point of evolution also has a part to play as will be illustrate through the next imaginary conversations between u_i and the successful contender u_R after being awarded the EStS fitness pay-off:

1. “ You just got lucky, odds are it won’t happen again...”

This situation could mean that evolution started at an evolutionary ‘blind spot’, a strategy that was not come by through a series of CSS’s but, provided there are no perturbations in its value, is surrounded by strategies with either equal or negative fitnesses. A slight perturbation in u_R in any direction will change its fate, sending evolution off into another direction which also means that it cannot evolve from a random evolutionary starting point. Nowak and Sigmund termed this situation a ‘Garden of Eden’ in 1989 [37].

$$\text{EStS only} = \text{Garden of Eden} \quad (2.10)$$

2. “ You made it this far, but you are not the only one...”

Here u_R cannot be reached through a series of CSS’s from just any evolutionary starting point. Sometimes the EStS can only be reached from one side or from both but with strategies on the way that are equivalent to u_R , compromising u_R ’s exclusivity. The CSS path will not end in a NIS as a slight perturbation in u_R , once it has reached an EStS, in the wrong direction might change its fate to that of an EBP, tying with neighborhood strategies. [84].

$$\text{compromised CSS} + \text{EStS} \rightarrow \text{EBP} \quad (2.11)$$

2.2 Adaptive Dynamics and the Rules of the ESS Game

In the field of ecology, continuous trait evolutionary games branched into two directions. The one branch adapted the game rules and tools to answer specific ecological questions and the other focused mostly on the dynamical aspects of the game, representing the game with a mathematical equation where parameters are assigned to the behavioral properties of interest. The mathematical branch was renamed adaptive dynamics or evolutionary invasion analysis (AD) and made the identification of evolutionary equilibriums such as the ESS more reliant on mathematical formulations [78, 35]. Both branches however share similar if not identical definitions to the long term evolutionary outcomes of the game [78, 42].

AD is a collection of techniques developed to model the possible long term outcomes (evolution) of interesting processes. They were developed during the 1990's by Metz *et al* for tracking or understanding the eventual consequences of small mutations in, amongst other properties, the strategies used by a species in playing the evolutionary game [16, 84, 48, 82]. The first step is defining the canonical equation⁵ which is the simplest mathematical representation of the process under investigation. In this study the process under investigation is the evolution of the competing strategies in a population which takes place by ways of a number of filtering rounds (games) between two contesting parties carrying strategies that differ very slightly from each other. Before constructing such an equation, it will be necessary to decide if the process is one where natural selection favors the contestants' frequencies or the strategies they are using.

2.2.1 Frequency Selection

Frequency dependent selection refers to the evolutionary process where the fitness of a phenotype, that is, a particular gene or set of genes responsible for a specific trait/strategy of (and defining) an individual⁶, is dependent on how often the phenotype appears (frequency) in the population in comparison to the other phenotypes present [4]. It results from the interaction between different species or between members of the same species with a slight variation in the genes responsible for addressing the same observable trait or strategy [33]. It can be labeled positive if the fitness of a phenotype is proportionate to its frequency and negative if it is inversely proportionate to its frequency. Ronald Fisher's observation that the sex ratio of some mammal species remain balanced even though most of the males never mate is an ex-

⁵Differential or difference equation modeling the process of interest

⁶And is a heritable characteristic that can be propagated into future offspring.

ample of negative frequency dependent selection. An increase in the male population will spark an increase in the female population (and not the male population) in the next generation keeping the balance [47]. Frequency dependent selection can result in a polymorphism⁷ if there is a coexistence between the members of the population and contributes towards the biodiversity of the species [16]. A population is labeled monomorphic when there is no phenotypic variation [82]. The existence of protected polymorphisms are not uncommon and can be either:

1. Stabilizing, where genetic diversity decreases as the population stabilizes on a specific strategy, usually the most common one used, and the population is then once again monomorphic or
2. Disruptive, where parties with extreme traits in comparison to the norm can independently evolve and lead to evolutionary branching [48, 36].

2.2.2 Strategy selection

Strategy selection on the other hand favors the best strategy. Even if the population is very small, but the strategy it plays is the best for the current circumstances, the population will outgrow the current resident. It is an exercise in strategy optimization and will therefore not leave room for a polymorphism[36]. This study is dedicated to the latter where the AD approach in this study will assume that:

1. The strategy is scalar valued and mathematically representable in which case graphical tools such as pairwise invisibility plots (PIPs) can be used to predict or explain evolutionary outcomes. PIP plots are a two dimensional representation of the outcomes of the competition model between two variants of the same population with a slight variation in their strategy parameter [84].
2. Evolution is ascribed to slight mutations in a monomorphic asexual population [34].
3. Strategy changes in the optimization process are small, discrete and far and few between allowing for the winning population to reach an equilibrium (ESiS) and the loser to exit the dynamics before the next challenger appears ready for the next round.
4. The population X and the strategy u do not share the same time scale. $X(n)$ will show the population density at time n which was achieved through the strategy $u(T)$ where T is the evolution time scale that can span several n 's. T

⁷Different versions of the same trait.

ticks a click only when its owner loses against the next successful challenger, but n ticks on at a constant interval pace.

5. The fitness proxy $\mathcal{R}(n)$ will be used to take the place of the intrinsic rate of natural increase r_M in the fitness analysis of a population as it will lead to similar conclusions [84, 85, 84].
6. The tournament ends when evolution ends in an ESS as described by (2.9).

The analysis of a typical game in the filtering process of the tournament between two contestants starts with the difference equation version of the differential equation suggested by Crow and Kimura in 1970. It simulates the population's progress from one time step to the next in a habitat E with carrying capacity \mathcal{K} and is given by [31]:

$$X(n+1) = \mathcal{R}(u(T), X(n), \mathcal{K})X(n) \quad (2.12)$$

where $X(n)$ is the population density at time n and is scaled according to the habitat capacity $\mathcal{K} = 1$. $u(T)$ is the new resident strategy at time n after winning the game against $u(T-1)$ and $\mathcal{R}_T(n)$ is the growth rate function, growth factor or fitness function and defines the fitness of the population generated by $u(T)$ at time n [31, 107, 6, 7]. Unless the discussion directly implicates \mathcal{K} in the deterministic environment, reference to \mathcal{K} can be omitted from (2.12).

2.3 The Competition Model

The discussions in the previous section will be made more mathematical here, paving the way towards a workable algorithm for the calculation of the ESS. For ease of notation, we put

$$u(T) = u_R \quad \text{the current residential strategy} \quad (2.13)$$

$$u(T+1) = u_M \quad \text{the next winning strategy} \quad (2.14)$$

Their associated populations will be shown as X_R and X_M respectively and the fitness function for u_R and u_M respectively will be shown as \mathcal{R} and \mathcal{M} . If a prospective challenger $x_M \ll 1$ (with population potential X_M) enters the zero fitness environment defined by the current winner (resident) X_R , the canonical equations setting the stage for the game that will follow is:

$$X_R(n+1) = \mathcal{R}(u_R, X_R(n) + x_M(n)) X_R(n) \approx \mathcal{R}(u_R, X_R(n)) X_R(n) \quad (2.15)$$

$$x_M(n+1) = \mathcal{M}(u_M, x_M(n) + X_R(n)) x_M(n) \approx \mathcal{M}(u_M, X_R(n)) x_M(n) \quad (2.16)$$

since $x_M \ll 1$ is very small and its contribution to the combined population total is negligible. At this point there are two points worth mentioning:

1. X_R is an established population, a small change in \mathcal{R} will not cause immediate extinction.
2. x_M is an initially small and fragile population, but if they practice a more suitable strategy such that $\mathcal{M} > 1$, x_M will evolve to a less fragile X_M . \mathcal{M} represents the fitness of the challenger in the environment defined by the already established X_R and is referred to as the invasion fitness function [37, 84].

The two interacting strategies are ready to interact but before the games can begin, a visit to the notation desk will be necessary:

$$\mathcal{R}(u_R, X_R) = (\mathcal{R}) \quad (2.17)$$

$$\frac{\partial}{\partial u_R} \mathcal{R}(u_R, X_R) = (\mathcal{R})_{u_R} \quad (2.18)$$

$$\frac{\partial^2}{\partial u_R^2} \mathcal{R}(u_R, X_R) = (\mathcal{R})_{u_R u_R} \quad (2.19)$$

$$\frac{\partial^2}{\partial u_R \partial X_R} \mathcal{R}(u_R, X_R) = (\mathcal{R})_{u_R X_R} \quad (2.20)$$

$$\mathcal{M}(u_M, X_M) = (\mathcal{M}) \quad (2.21)$$

$$\frac{\partial}{\partial X_M} \mathcal{M}(u_M, X_M) = (\mathcal{M})_{X_M} \quad (2.22)$$

$$\frac{\partial^2}{\partial X_M^2} \mathcal{M}(u_M, X_M) = (\mathcal{M})_{X_M X_M} \quad (2.23)$$

$$\frac{\partial^2}{\partial X_M \partial u_M} \mathcal{M}(u_M, X_M) = (\mathcal{M})_{X_M u_M} \quad (2.24)$$

When evaluations of () are done at (u^*, X^*) , it will be indicated by the notation ()^{*} and when evaluations are done at some common point (u_o, X_o) , it will be indicated by ()^o. The first derivative of \mathcal{R} with respect to the strategy u_R (2.18) is referred to as the fitness gradient of \mathcal{R} [48].

2.3.1 The resident

The resident population X_R is at an ESis⁸ at this time showing zero fitness⁹ [16, 48]:

$$(\mathcal{R}) = 1 \quad (2.25)$$

⁸Demographic attractors under zero stress

⁹Zero intent of increase or decrease

$$(\mathcal{R})_{u_R} = 0 \quad (2.26)$$

As \mathcal{R} and \mathcal{M} are identical operators except for the values of X and u , equation (2.16) suggests a strategy switch in (2.15) to evaluate the optimizing abilities of u_M when an established population X_R is exposed to it. With that in mind, the strategy u_R in (2.15) is switched with u_M and the instantaneous change in $\mathcal{R}(u_M, X_R)$ recorded. Clearly, the resident will move off its ESiS $\mathcal{R} = 1$, but where to? The analysis will now take on two approaches, the first is a simulation of natural selection and the second an intuitive approach as to what is meant by an optimal strategy specifically for the Shepherd function.

1. Natural selection:

Suppose the new strategy $u_M = u_R + h_u$ raises the fitness of \mathcal{R} to values above one, then (2.15) changes to:

$$1 < \mathcal{R}(u_M, X_R) \quad (2.27)$$

$$1 < \mathcal{R}(u_R + h_u, X_R) \quad (2.28)$$

$$1 < (\mathcal{R}) + (\mathcal{R})_{u_R} \cdot h_u \quad (2.29)$$

$$1 < 1 + (\mathcal{R})_{u_R} \cdot (u_M - u_R) \quad (2.30)$$

$$0 < (\mathcal{R})_{u_R} \cdot (u_M - u_R) \quad (2.31)$$

The Taylor expansion in two variables was used in (2.29) omitting terms containing h_u^2 and higher and putting $\mathcal{R} = 1$ (ESiS). In (2.31) the slope of the fitness generating function \mathcal{R} at u_R is shown as $(\mathcal{R})_{u_R}$, referred to in this context as the fitness gradient. Equation (2.31) reveals that on the u_R axes:

$$\text{if } u_R < u_M \text{ then } (\mathcal{R})_{u_R} > 0 \quad (2.32)$$

$$\text{and if } u_R > u_M \text{ then } (\mathcal{R})_{u_R} < 0 \quad (2.33)$$

Evolution will follow the strategy u_M that boosts the fitness function of the residential strategy and the fitness gradient of the residential strategy evaluated at u_R will point in the direction of the better strategy u_M . Natural selection will then favor a next challenger with strategy $u_R + h$ in the ‘better strategy direction’. Figure 2.1(a) shows the instantaneous change in \mathcal{R} from its horizontal ESiS position when its strategy u_R is switched with u_M in \mathcal{R} .

2. $(\mathcal{R})^*$ a maximum:

Suppose that climbing the (CSS) ladder to ever better strategies is not an

endless process and has come to a strategy $u_M = u^*$ which will become the new resident $u_R = u^*$ with ESiS characteristics:

$$(\mathcal{R})^* = 1 \quad (2.34)$$

$$(\mathcal{R})_{u_R}^* = 0, \quad (2.35)$$

where exposure to a next strategy on the evolutionary axes either causes zero or negative growth in the fitness function \mathcal{R} . This could indicate a halt in evolution either because u^* is the ESS and therefore every next new strategy will meet the same fate, or because evolution has landed on a plateau of strategies capable of evolving a similar population scattering about \mathcal{K} . The latter case will result in EBP's and polymorphisms. Since both cases can be characterized by an ascent of CSS's, differentiating between them cannot follow just from the testing of $(\mathcal{R})_{u_R}^*$. For u^* to be exclusive it will further be required that subjecting X^* to any other neighborhood strategy u_R , through a strategy switch, should cause negative growth patterns in $\mathcal{R}(u_R, X^*)$, either by inducing extreme behavior in X^* or by damping the oscillations of X^* , but whatever the situation, it must not result in zero fitness as this would indicate a strategy tie. From the discussion of the Shepherd model in Chapter 1, it was seen that a strategy u evolves a population X that oscillates about \mathcal{K} , reaching values either side or less than \mathcal{K} with a variation in extremity. In the extreme case, if the optimal strategy u^* offers environmental advantages superior to that of u_R , then subjecting X^* to u_R should cause environmental disadvantages, aggravating population peaks above or below \mathcal{K} . From (1.32) and (1.33) aggravated behavior will occur if, when $X^* > \mathcal{K}$,

$$\left(\frac{X^*}{\mathcal{K}}\right)^{u_R} > \left(\frac{X^*}{\mathcal{K}}\right)^{u^*} \quad (2.36)$$

increasing the value u^* would have generated, and, for $X^* < \mathcal{K}$,

$$\left(\frac{X^*}{\mathcal{K}}\right)^{u_R} < \left(\frac{X^*}{\mathcal{K}}\right)^{u^*} \quad (2.37)$$

decreasing the value u^* would have generated. Both cases are satisfied when $u_R > u^*$. For damping behavior, u_R must suppress oscillations in X^* , that is, when $X^* > \mathcal{K}$,

$$\left(\frac{X^*}{\mathcal{K}}\right)^{u_R} < \left(\frac{X^*}{\mathcal{K}}\right)^{u^*} \quad (2.38)$$

suppressing the larger value associated with u^* and when $X^* < \mathcal{K}$,

$$\left(\frac{X^*}{\mathcal{K}}\right)^{u_R} > \left(\frac{X^*}{\mathcal{K}}\right)^{u^*}, \quad (2.39)$$

suppressing the smaller value associated with u^* . Both cases are possible when $u_R < u^*$. The conclusion that can be made here is that, for the Shepherd function, strategy values less than u^* generate damped populations and strategy values larger generate more extreme oscillatory populations; so what makes u^* a more optimal strategy? When exposing the population X^* describing the oscillation about \mathcal{K} generated by u^* to other neighborhood strategies u_R , the fitness function $\mathcal{R}(u_R, X^*)$ or the invasion exponent I describing one period about \mathcal{K} , must show negative fitness, while at u^* , the combination remains one, which, from the previous section, describes a CSS. Repeated iterations will of course change X^* into X_R , which is why the optimum test relies on the outcome of the \mathcal{R} 's describing one period or alternatively the invasion exponent I as described in (2.4). As discussed before, the CSS path shows fitness increments all the way to u^* , therefore, the further away the CSS strategies are from u^* , the more 'negative' the $\mathcal{R}(u_R, X^*)$ combinations will be. On account of this observation, $u_R = u^*$ represents a maximum for $\mathcal{R}(u_R, X^*)$ or I and the following addition can be made to equations (2.34) and (2.35):

$$(\mathcal{R})_{u_R u_R}^* < 0 \quad (2.40)$$

$$\text{or } (I)_{u_R u_R}^* < 0 \quad (2.41)$$

2.3.2 The challenger

What will u^* represent for \mathcal{M} ? Equation (2.16) shows that the established residential population X_R is exposed to the strategy u_M which can either result in $\mathcal{M} > 1$ thereby boosting the fragile population x_M or $\mathcal{M} < 1$ whereby x_M will go extinct quickly. Recall from Chapter 1 that the fitness function decreases (from a maximum value of r) as the population increases and will abruptly slow down or even become negative once $X_R > \mathcal{K}$. Therefore, from (1.32) and (1.33), $\mathcal{M}(u_M, X_R) > 1$ only if the strategy u_R did not evolve an optimal population for the environment defined by \mathcal{K} .

1. Natural selection:

In other words, if exposing X_R to u_M results in positive fitness for $\mathcal{M}(u_M, X_R)$ and evolves the population $X_M = X_R + h_X$ then:

$$1 < \mathcal{M}(u_M, X_R) \quad (2.42)$$

$$1 < \mathcal{M}(u_M, X_M - h_X) \quad (2.43)$$

$$1 < (\mathcal{M}) - (\mathcal{M})_{X_M} \cdot h_X \quad (2.44)$$

$$1 = 1 + (\mathcal{M})_{X_M} \cdot (X_R - X_M) \quad (2.45)$$

$$0 < (\mathcal{M})_{X_M} \cdot (X_R - X_M) \quad (2.46)$$

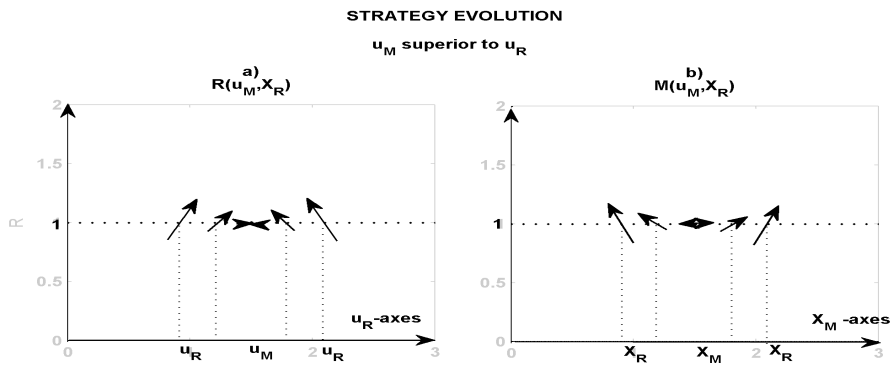


Figure 2.1: Figure (a) shows the initial reaction in \mathcal{R} after switching its residential strategy u_R with the competitor strategy u_M . The arrows indicate the path evolution will follow if u_M proves to be a better strategy than u_R . The closer u_R is to u_M , the smaller the rate of change in \mathcal{R} as the difference between $\mathcal{R}(u_R)$ and $\mathcal{R}(u_M)$ is less. Figure (b) shows that the further away the residential population is from a more optimal population the better strategy u_M can generate, the higher the initial growth rate in \mathcal{M} will be.

Which can be visualized on the X_M axes, under the rule of u_M , as the study of what happens to \mathcal{M} when a population evolved at a different strategy u_R is

exposed to the strategy u_M :

$$\text{If } X_R > X_M \text{ then } (\mathcal{M})_{X_M} > 0 \quad (2.47)$$

$$\text{and if } X_R < X_M \text{ then } (\mathcal{M})_{X_M} < 0 \quad (2.48)$$

There is an increase in the growth of \mathcal{M} when exposing inferior populations to u_M . Figure 2.1(b) shows the instantaneous change in \mathcal{M} when the ESis population X_M is replaced by X_R in \mathcal{M} .

2. $(\mathcal{M})^*$ a minimum:

From the previous discussion, the CSS strategy u^* is one such that, when X^* was exposed to other strategies u_R over one period, the periodic combination of the $\mathcal{R}(u_R, X^*)$'s resulted in negative growth. If the challenger u_M is the ESS strategy u^* then (2.42) must be true for all $X_R \neq X^*$, even when X^* is at a very low density $X^* \ll 1$. Again, since this can only happen during one period and X^* is very small,

$$\mathcal{M}(u^*, X_R) \gg 1 \quad (2.49)$$

for $X^* \ll 1$ to evolve quickly enough to secure its position. From (2.8), u^* is then a NIS. From the conclusions made concerning $\left(\frac{X^*}{\mathcal{K}}\right)^{u_R}$ that u_R would either aggravate or damp the optimal oscillation pattern defined by X^* , the opposite will be true for $\left(\frac{X_R}{\mathcal{K}}\right)^{u^*}$. The fitness function \mathcal{M} with optimal strategy u^* should over one period's exposure to X_R , show positive fitness, and excessively so! The less optimal X_R is, the greater the effect u^* will have and better the chances are of \mathcal{M} being large enough. Therefore, not only does $\mathcal{M}(X_R, u^*)$ represent a minimum at $X_R = X^*$ but will only be positive enough if the different strategies around u^* generate populations with distinctly different oscillation patterns about \mathcal{K} , where those to the left generate increasingly lessor oscillatory behavior and those to the right, increasingly more erratic patterns. This can be seen in Figures 2.2(a) and (b) where (a) shows a situation where there is a slight variation as u_R is increase, with $u_R = 8.9595$ representing the optimal strategy (CSS) for \mathcal{R} but since the variation is not very distinct, this strategy does not define a minimum for \mathcal{M} , and is therefore not an ESS. Figure (b) on the other hand shows more distinct variations in the pattern as u_R is increased, therefore $u^* = 5.904$ defines both a maximum for \mathcal{R} and a minimum for \mathcal{M} and is an ESS.

2.3.3 The combination

The properties of \mathcal{R} and \mathcal{M} can be combined (in the gaming arena) in a single fitness function \mathfrak{R} when the above analysis is converted into a pure study of opposing

strategies, replacing all reference to the population with the strategy responsible for its evolution:

$$\text{evaluation points: } (u_M, X_R) \equiv (u_M, u_R) \quad (2.50)$$

$$\text{derivatives: } (\)_{X_M} \equiv (\)_{u_M} \quad (2.51)$$

For the three dimensional axes (u_M, u_R, \mathfrak{R}) a second trip to the notation desk will be necessary:

$$(\mathfrak{R}) = \mathfrak{R}(u_M, u_R) \quad (2.52)$$

$$(\mathfrak{R})^o = \mathfrak{R}(u_M, u_R) \text{ when } u_M = u_R \quad (2.53)$$

$$(\mathfrak{R})^* = \mathfrak{R}(u_M, u_R) \text{ when } u_M = u_R = u^* \quad (2.54)$$

The properties of \mathcal{R} and \mathcal{M} can then be combined as:

$$(\mathfrak{R})^* = 1 \quad (2.55)$$

$$(\mathfrak{R})_{u_R}^* = 0 \quad (2.56)$$

$$(\mathfrak{R})_{u_M}^* = 0 \quad (2.57)$$

$$(\mathfrak{R})_{u_R u_R}^* < 0 \quad (2.58)$$

$$(\mathfrak{R})_{u_M u_M}^* > 0 \quad (2.59)$$

2.3.4 The fundamental theorem of natural selection

From the extension of the *Fundamental Theorem of Natural Selection* to evolving strategies, the rate at which the value of a currently dominating strategy u_R (that brought the population to an equilibrium with population X_R) evolves is both in the direction of and proportional to the local fitness gradient of the resident evaluated at the dominant residential strategy [104]. It simply means that if the fitness gradient is positive and large, then the direction of strategy improvement is to the right at an accelerated rate proportionate to the magnitude of the gradient evaluated at $u_M = u_R$. As a differential equation the fundamental theorem has the representation [47, 38, 98, 55]:

$$\frac{d}{dt}u_R(t) = \frac{1}{2}\mu\sigma^2 X_R(t)(u_R(t)) (\mathfrak{R}(t))_{u_R}^o \quad (2.60)$$

$$= k (\mathfrak{R}(t))_{u_R}^o \quad (2.61)$$

$$\text{where } k = \frac{1}{2}\mu\sigma^2 X_R(t) \quad (2.62)$$

The interpretation of the symbols in equation (2.60) are:

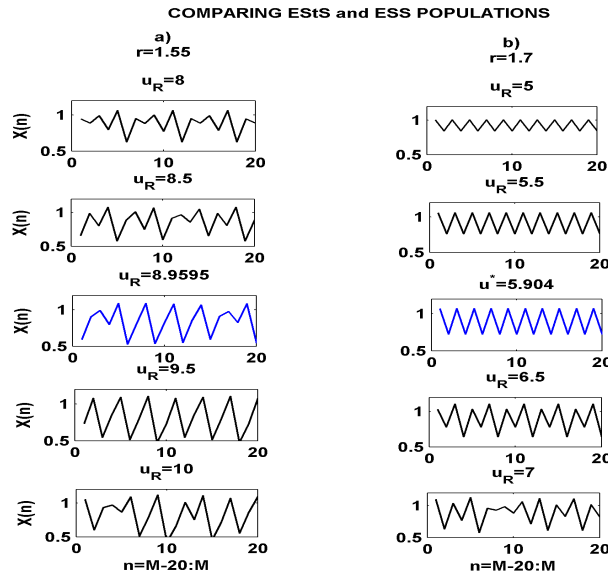


Figure 2.2: (a) The populations X_R were generated for a range of u_R values to the left and right of the CSS $u_R = 8.9595$. The variation in population patterns are very small. (b) Larger variations in the population pattern, ranging from small oscillations to large oscillations with $u^* = 5.904$ offering the better fit and defining an ESS.

1. μX_R : The evolutionary process of the strategy is a function of how often challengers present themselves, where μ is the per capita mutation rate and X_R is the population size generated with strategy u_R .
2. σ^2 : The evolutionary process of the strategy is a function of the variance of mu-

tation effects, where, for instance, a larger variance (larger gradient magnitude) will correspond to an increase in the evolution rate.

3. $(\mathfrak{R}(t))_{u_R}$ evaluated at $u_R(t) = u_M(t)$: Evaluating the gradient around the dominant strategy shows the relative fitness advantage of the next challenger strategy over the dominant strategy $u_R(t)$. The steeper the gradient, the faster the evolution to higher values when positive and lower when negative.
4. $\frac{1}{2}$: a scaling factor (in this case $\frac{1}{2}$) as the equation was derived for a monomorphic population at equilibrium and the evolution of the dominant strategy is very small and subjected to directional¹⁰ selection where only half will go into the ‘right’ direction which is the successfully replacement of the dominant strategy.

The evolutionary process will come to a stop when the fitness gradient is zero:

$$(\mathfrak{R}(t))_{u_R}^o = 0 \quad (2.63)$$

A zero fitness gradient implies that the two competing strategies are on par, neither having an advantage over the other and could indicate the end of evolution. As equation (2.60) gives a simple mathematical representation of the process under investigation, it is also referred to as the canonical equation of AD [34, 23, 124]. In conclusion, k in (2.61) defines the ‘speed’ of convergence to an EStS say u^* when $(\mathfrak{R})_{u_R}^o$ is a decreasing function of the next round winners, that is, (2.60) converges to u^* when the magnitude of the initial fitness gradient progressively grows smaller and disappear altogether as u^* is approached. The fitness gradient is therefore a decreasing function of u_R :

$$\frac{d}{du_R} (\mathfrak{R})_{u_R}^o < 0 \quad (2.64)$$

$$(\mathfrak{R})_{u_R u_R}^o + (\mathfrak{R})_{u_M u_R}^o \cdot (u_M)_{u_R}^o < 0 \quad (2.65)$$

Since the fitness gradient is evaluated at $u_M = u_R$, $(u_M)_{u_R} = 1$ and equation (2.65) is the equation:

$$(\mathfrak{R})_{u_R u_R}^o + (\mathfrak{R})_{u_M u_R}^o < 0 \quad (2.66)$$

The fitness gradient $(\mathfrak{R})_{u_M}$ evaluated at $u_M = u_R$ will show a fitness disadvantage of u_R over u_M (the opposite of (2.60)). It will have the opposite effect to the CSS

¹⁰When natural selection favors a specific strategy [20]

convergence, looking at evolution in reverse, showing by how much, when u_R moves further away from u^* , the population would show (increasingly) an increase in fitness when they are exposed to u^* . The gradient $(\mathfrak{R})_{u_M}^o$ will therefore be a diverging function of evolution in reverse (when moving further away from u^*), that is:

$$\frac{d}{du_M} (\mathfrak{R})_{u_M}^o > 0 \quad (2.67)$$

Using similar conclusions as in (2.66),

$$(\mathfrak{R})_{u_M u_M}^o + (\mathfrak{R})_{u_M u_R}^o > 0 \quad (2.68)$$

2.4 The ESS Criteria

Establishing whether u_R is the champion, or similarly, if u_M will be the champion ESS u^* with associate population X^* it will be required that u_R with associated X_R pass the following four check points taken from the EGT formulation in (2.9) as well as the discussions in the previous section [81, 41, 8]:

finite CSS series + EStS + NIS = ESS

1. **Check point 1: To be an ESS, $u_R = u^*$ must primarily be an ESiS**
 u_R must be an equilibrium strategy in the absence of competition:

$$(\mathfrak{R})^* = 1 \quad (2.69)$$

Showing a zero fitness gradient in the u_R direction on the combined axes:

$$(\mathfrak{R})_{u_R}^* = 0 \quad (2.70)$$

2. **Check point 2: $u_R = u^*$ must be a CSS**

The strategy u^* is a CSS if exposing X^* to any other neighborhood strategy u_M causes a decrease in X^*

$$(\mathfrak{R})_{u_R u_R}^* < 0 \quad (2.71)$$

3. **Check point 3: $u_M = u^*$ must be a NIS**

The strategy u^* is a NIS if it boosts the fitness functions of populations evolved at different strategies (in the neighborhood of u^*) when these populations are exposed to u^* leaving no possibilities of a tie.

$$(\mathfrak{R})_{u_M u_M}^* > 0 \quad (2.72)$$

4. Check point 4: Evolution must come to a halt at u^*

Subtracting the CSS and NIS equations (2.66) - (2.68) and realizing that the mixed derivatives in both are the same at $u_M = u_R = u^*$ gives a relationship that combines the CSS (steady) convergence and the NIS (stability) as the evolutionary halt:

$$(\mathfrak{R})_{u_R u_R}^* < (\mathfrak{R})_{u_M u_M}^* \quad (2.73)$$

The combined graphical implication of the end of evolution comes from the classroom equations:

$$M1 = (\mathfrak{R})_{u_R} \quad (2.74)$$

$$M2 = (\mathfrak{R})_{u_M} \quad (2.75)$$

$$M = \left((\mathfrak{R})_{u_R u_R} \right) \left((\mathfrak{R})_{u_M u_M} \right) - \left((\mathfrak{R})_{u_M u_R} \right)^2 \quad (2.76)$$

From equations (2.56) till (2.59), equation (2.76) evaluated at the coordinate (u^*, u^*) will result in $M1 = 0$, $M2 = 0$ and $M < 0$ which represent the location of a saddle point [113]. The algorithm for strategy optimization in Chapter 4 will test u^* according to these criteria.

2.5 Summary of Acronyms and Terminology

1. Density dependent models (**DDM's**) are models equipped with a mechanism that can accelerate growth rates at low densities and decelerate growth rates as densities become critical.
2. Evolutionary Game Theory (**EGT**) is the study of evolutionary processes such as evolving strategies within populations [74, 76].
3. Adaptive Dynamics (**AD**) is a collection of techniques developed to model the possible long term outcomes of evolutionary processes [16, 84, 48, 82].
4. **Fitness** is defined as the 'hypothetical average rate of exponential growth', which results from the thought experiment in which a clone of the type under consideration grows in an ergodic environment [85].
5. **Environment** includes all factors that can potentially influence a population's own behavior, be it non living such as weather (abiotic) or living such as predators and densities (biotic) [85].

6. The fitness function ($\mathcal{R}(n)$) represents the growth potential of a residential population X over a time interval under investigation and is, in this study, a function of the strategy (u) practiced by the population as well as the maximum population density the environment can accommodate without the risk of exploitation (\mathcal{K}) [82, 84, 82, 109]. The sign of the fitness gradient (\mathcal{R}_{u_R}) points to the next strategy in strategy evolution [48].
7. The invasion fitness function (\mathcal{M}) is the fitness function of the challenger in the environment defined by the established resident [37, 84].
8. An evolutionary game evolves when the fitness of an individual is challenged by not only its own strategy but by the strategies of others as well as environment limitations. Such a game can last up to several rounds with the evolutionary time scale T ticking a click only with the (few and far between) arrival of an even better strategist. The better strategist is then awarded the fitness pay-off and becomes the new resident ready for the next round. There are now a few possibilities regarding the resident strategy that will be relative to this study:
 - (a) It is an evolutionary singular strategy (**ESiS**) which is a strategy that evolves a population to an equilibrium followed by a zero fitness in the absence of competition until such time as the next competitor challenges the status quo [84].
 - (b) It can be a convergent stable strategy (**CSS**) which is a strategy in a series of strategies converging to some evolutionary attractor [27, 117].
 - (c) It can be an evolutionary steady strategy (**EStS**) which is one, in terms of environment and fitness, that dominates and defines an environment (with zero fitness) where all other contenders of the same type using a slight variation of this strategy will not have positive fitness when competing with the EStS but can share equilibrium status with the EStS [85, 84].
 - (d) It can be a neighborhood invasion strategy (**NIS**) where, when evaluated in evolutionary reverse, all other neighborhood strategists further away will show increasingly positive fitnesses when their strategies are interchanged with the ESS strategy [6, 8].
 - (e) It can be an evolutionary stable strategy (**ESS**) which is an evolutionary attractor come by a series of CSS strategies ending in an ESiS that is also an EStS and a NIS. The CSS indicates non invasibility of an established X^* , a NIS indicates non invasibility of X^* at very small densities and an ESS non invasibility in both cases.

- (f) It can be an evolutionary branching point (**EBP**) which is an EStS that, after a slight perturbation in its value, will not be driven back to the EStS but will instead result in a non converging quest or strategy ties with two (or even more) sub populations evolving [37].

“Anyway, you need people of intelligence on this sort of mission .. quest .. thing.”

“Well, that rules you out, Pip!” - Lord of the Rings, J.R.R. Tolkien

Chapter 3

The Age-Structured Model

Designing an age-structured population model requires knowledge of the interaction between age and time related phenomena within the population. For instance, both age of maturity and age of mortality are present at the same time in the population dynamics. The information required to facilitate an age-structured model can be tapped from life tables, which is an account of the change in population density in the different age groups over time. It can be used to estimate survival and birth rates as well as other tendencies such as signs of intervention strategies in population densities. Since the females are mostly responsible for density intervention, the model will be tailor designed around their ability to control the densities of the recruitment population by either over or under dispersing them on resources and so staying within the bounds of the environment.

3.1 The Shepherd Recruitment Function

In this chapter an age-structured model will be designed for a population exercising density control at the recruitment level. The recruits will be exposed to the Shepherd density curbing mechanism leaving the other age groups to evolve from this in a linear fashion. The Shepherd mechanism can also be used to model density issues in a population as a whole as was done by Cisneros-Mata *et al* [91]. After defining the model and assigning a scalar value to the strategy associated with density control, it will be exposed to periodic scenarios followed by strategy optimization. In the non age-structured case the \mathcal{R} notation was used to describe the change in the population from one time step to the next, and this notation will be carried through to the age-structured case except that it will not be the Shepherd density function itself but rather a combination of all the factors contributing towards the change. The Shepherd density function will be limited to the recruitment level and will simulate

the proportion $\psi(n)$ of recruits that successfully ‘graduate’ from the larva or egg stage where

$$\psi(n) = \frac{r}{1 + \left(\frac{X(n)}{\mathcal{K}}\right)^u} \quad (3.1)$$

The data will be scaled so that $\mathcal{K} = 1$ and $X(n)$ will refer to the density of the recruitment population where the females adopt a strategy u in response to environmental demand \mathcal{K} .

3.1.1 Defining age-structure

In an age-structured model, age classes can be measured discretely in either days, months or years depending on the nature of the species involved. The females in each age class are assigned reproductive and mortality rates according to the class they are in and the progress of the species is then calculated as the difference between the number of births and deaths from these different age classes. The females in age class i at time $n - 1$ in a population with m age classes will be represented by $x_i(n - 1)$, $i = 1, ..m$ and, following Getz [50], the number of individuals born from these females in all the age classes will be shown as the tally $X(n - 1)$. If the proportion $s_0(n - 1)$ of the new born tally $X(n - 1)$ survives to the first age class x_1 at time n , then:

$$x_1(n) = s_0(n - 1)X(n - 1) \quad (3.2)$$

This survival proportioning can be extended right through the age hierarchy as:

$$x_{i+1}(n) = s_i(n - 1)x_i(n - 1) \quad i = 1, ..m - 1 \quad (3.3)$$

If the number of individuals born from those females in age group i at time n is the proportion $b_i(n)x_i(n)$ then the next generation $X(n)$ is the sum:

$$X(n) = \sum_{i=1}^m b_i(n)x_i(n) \quad (3.4)$$

Equations (3.2) to (3.4) can also be expressed as a Leslie matrix and the population progress can be analyzed along this path as was done by, amongst others, Ferriere and Gatto 1993 and is shown next but will not be the approach of this study [46, 50, 45, 46].

$$\begin{pmatrix} x_1 \\ x_2 \\ \dots \\ x_m \end{pmatrix}_{(n)} = \begin{pmatrix} b_1 s_0 & b_2 s_0 & \dots & b_m s_0 \\ s_1 & 0 & \dots & 0 \\ 0 & s_2 & \dots & 0 \\ \dots & \dots & \dots & \dots \\ 0 & 0 & s_{m-1} & 0 \end{pmatrix}_{(n-1)} \begin{pmatrix} x_1 \\ x_2 \\ \dots \\ x_m \end{pmatrix}_{(n-1)}$$

$$X(n) = b_1(n)x_1(n) + b_2(n)x_2(n) + \dots + b_m(n)x_m(n)$$

The analysis in this study in establishing the nature and stability of certain attractors whether they are periodic, quasi periodic or chaotic will however be carried out on the all inclusive difference equation formulated from equations (3.2) to (3.4) as illustrated by Getz [50]:

1. Each age class can be expressed in terms of the new born tally X :

$$\begin{aligned} x_i(n) &= s_{i-1}(n-1)x_{i-1}(n-1) \\ &= s_{i-1}(n-1)s_{i-2}(n-2)x_{i-2}(n-2) \text{ from (3.3)} \\ &= \left(\prod_{k=0}^{i-1} s_k(n-i+k) \right) X(n-i) \text{ from (3.2)} \end{aligned}$$

2. Defining $L_{n-i} = \prod_{k=0}^{i-1} s_k(n-i+k)$, equation (3.3) can compactly be expressed as [50]

$$x_i(n) = L_{n-i}X(n-i) \quad i = 1, \dots, m \quad (3.5)$$

3. If each of the $x_i(n)$ in (3.5) contribute the proportion $b_i(n)x_i(n)$ towards the offspring tally $X(n)$ then

$$X(n) = \sum_{i=1}^m b_i(n)x_i(n) \quad (3.6)$$

$$= \sum_{i=1}^m b_i(n)L_{n-i}X(n-i) \quad (3.7)$$

3.1.2 Including density

A number of assumptions can now be made concerning the system variables $b_i(n)$ and $s_i(n)$ depending on the availability of data and an acceptable blend of accuracy and compromise [33]. Reproductive and mortality rates are indeed affected by population densities as limited resources will force a population to act more conservatively as opposed to their behavior in the presence of abundance. Since age-structure already adds a fair share of complications to the modeling process, a compromise will be made by allowing most of the system variables to be density independent. Deciding which variable should be made density dependent, comes from our choice of ‘interesting matters’ which in this study is also a realistic assumption. In the growth of larval fish, as researched by Shepherd and Cushing, it was observed that the recruits are most at risk and are therefore easier to manipulate by the females when it comes to environmental challenges [110]. A density mechanism should therefore be incorporated here. The system variables are then chosen as follows:

1. Compromise: If the post recruitment populations' reproductive and mortality components are unaffected by the population's density and do not change with time n , then

$$s_i(n) = s_i \quad \text{and} \quad b_i(n) = b_i \quad i = 1, 2, \dots, m \quad (3.8)$$

2. Accuracy: A density compromised recruitment survival coefficient $s_0(X(n), n)$ is suggested where

$$s_0(X(n), n) = s_o\psi(u, X(n)) = s_o\psi(n) \quad (3.9)$$

where s_o on the right represents the (now constant) proportion of the density curbed recruits that survive to age one. Equation (3.2) is then replaced by

$$x_1(n) = s_o\psi(n-1)X(n-1) \quad (3.10)$$

and equation (3.7) is then the more realistic non linear equation

$$X(n) = \sum_{i=1}^m b_i L_{i-1} \psi(n-i) X(n-i) \quad (3.11)$$

$$= \sum_{i=1}^m A_i \psi(n-i) X(n-i) \quad (3.12)$$

$$= \left(\sum_{i=1}^m A_i \psi(n-i) \frac{X(n-i)}{X(n-m)} \right) X(n-m) \quad (3.13)$$

$$= \mathcal{R}(u, \bar{X}(u)) X(n-m) \quad (3.14)$$

Where

$$A_i = b_i L_{i-1} \quad (3.15)$$

$$\psi(n) = \frac{r}{1 + (X(n))^{u(n)}} \quad (3.16)$$

$$\bar{X}(u) = [X(n-1), X(n-2), \dots, X(n-m)]_{\text{calculated at } u} \quad (3.17)$$

$$\mathcal{R}(u, \bar{X}(u)) = \left(\sum_{i=1}^m A_i \psi(n-i) \frac{X(n-i)}{X(n-m)} \right) \quad (3.18)$$

There are four points worth mentioning concerning (3.14) which will be useful in the planning of the \mathcal{R} -optimization algorithm:

1. There are other options for defining \mathcal{R} , instead of taking $X(n-m)$ out as a common factor on the right, one could also have used $X(n-1)$ for instance. It was however found during the programming of the above that the $X(n-m)$ version faithfully delivers an optimum where one existed.

2. To make a first next prediction on the state of $X(n)$, equation (3.14) requires m initial values

$$\bar{X}_I = [X(n-1), X(n-2), \dots, X(n-m)] \quad (3.19)$$

3. Instead of calculating \mathcal{R} directly, it will be easier to rather calculate the ratio

$$\mathcal{R}(u, \bar{X}(u)) = \frac{X(n)}{X(n-m)} \quad (3.20)$$

4. For the non age-structured case, $A_1 = b_1 s_o = 1$ will be the only non zero coefficient of (3.14).

3.2 Periodic Point Analysis

In this section the age-structured population model (3.12) will be analyzed to establish for which choices of the system coefficients A_i there will be periodic solutions. This study is also suited to the non age-structured model by making appropriate choices for A_i . Before the analysis starts it will be useful to first investigate the properties of the Shepherd recruitment function $\psi(n)$. It will be assumed in all that follows that $u > 1$, $X(n) > 0$ and $\psi(n) = \frac{r}{1+(X(n))^u}$:

- 1.

$$0 < \psi(n) < r \quad (3.21)$$

- 2.

$$(X(n))^u = \frac{r}{\psi(n)} - 1 \quad (3.22)$$

- 3.

$$\begin{aligned} (\psi(n))_{u_R} &= -\frac{1}{r} \psi^2(n) (X(n))^u \ln(X(n)) \\ &= -\frac{1}{r} \psi(n) (r - \psi(n)) \ln(X(n)) \end{aligned} \quad (3.23)$$

- 4.

$$\ln(X(n)) = -\frac{r}{\psi(r - \psi(n))} (\psi(n))_{u_R} \quad \text{from (3.23)} \quad (3.24)$$

- 5.

$$(\psi(n))_{u_R u_R} = -\frac{(r - 2\psi(n)) \ln(X(n))}{r} (\psi(n))_{u_R} \quad (3.25)$$

$$= \frac{(r - 2\psi(n))}{\psi(r - \psi(n))} \left((\psi(n))_{u_R} \right)^2 \quad \text{using (3.24)} \quad (3.26)$$

3.2.1 Is a fixed point solution possible?

For a fixed point solution to (3.12), $X(n) = X(1) \forall n$ with corresponding

$$\psi(X(n)) = \psi(X(1)) = \psi(1) \forall n \quad (3.27)$$

$$\text{where } A = \sum_{i=1}^m A_i, \quad (3.28)$$

Equation (3.12) then simplifies to:

$$X(1) = \left(\sum_{i=1}^m A_i \right) \psi(1) X(1) \quad (3.29)$$

$$= A\psi(1) X(1) \quad (3.30)$$

$$= \mathcal{R}(u, \bar{X}(u))X(1) \quad (3.31)$$

$$\text{where } \mathcal{R}(u, \bar{X}(u)) = A\psi(1) \quad (3.32)$$

Theorem 3.1 *There are no fixed point solutions for (3.12).*

To prove this statement, (3.32) will be subjected to the first two check points of Chapter 2:

1. Check point 1:

From (2.69) and (2.70) a fixed point is characterized by $\mathcal{R} = 1$ and $(\mathcal{R})_{u_R} = 0$:

$$\begin{aligned} \psi(1) &= \frac{1}{A} \\ \frac{r}{1 + (X(1))^u} &= \frac{1}{A} \\ (X(1))^u &= rA - 1 \end{aligned} \quad (3.33)$$

The first derivative with respect to u :

$$(\mathcal{R})_{u_R} = A(\psi(1))_{u_R} \quad (3.34)$$

The above can only be zero if the derivative of ψ is zero and from (3.23) this is only possible if $X(1) = 1$, limiting r in (3.33) to $r = \frac{2}{A}$ and $\psi(1) = \frac{r}{2}$.

2. Check point 2:

Additionally to check point 1, (2.71) requires that $(\mathcal{R})_{u_R u_R} < 0$:

$$(\mathcal{R})_{u_R u_R} = A(\psi(1))_{u_R u_R} \quad (3.35)$$

Equations (3.23) and (3.25) show that if $X(1) = 1$, the second derivative of \mathcal{R} is zero which is a saddle point and not the required maximum. It can therefore be concluded that no optimal strategies are possible for a constant population $X(n) = X(1) \forall n$ in equation (3.12).

3.2.2 Model parameters conducive to a period two solution

For a period two fixed point we put

$$X(n) = X(n - 2i) = X(1) \quad (3.36)$$

$$X(n - 1) = X(n - (2i + 1)) = X(2) \quad \forall i = 1, 2, \dots \quad (3.37)$$

with corresponding $\psi(1)$ and $\psi(2)$. Equation (3.12) then takes the form:

$$X(1) = \left(\sum_{i=1}^{M/2} A_{2i-1} \right) \psi(2)X(2) + \left(\sum_{i=1}^{M/2} A_{2i} \right) \psi(1)X(1) \quad (3.38)$$

$$= C\psi(2)X(2) + B\psi(1)X(1) \quad (3.39)$$

$$\text{where } C = \sum_{i=1}^{M/2} A_{2i-1} \text{ and } B = \sum_{i=1}^{M/2} A_{2i} \quad (3.40)$$

$$X(1)(1 - B\psi(1)) = C\psi(2)X(2) \quad (3.41)$$

$$X(1) = \frac{C\psi(2)}{1 - B\psi(1)}X(2) \quad (3.42)$$

$$= \mathcal{R}(2)X(2) \quad (3.43)$$

Where $M = m$ when m is even and $M = m + 1$ when m is odd. In general,

$$X(n + 1) = \mathcal{R}(n)X(n) \quad n = 1, 2 \quad (3.44)$$

$$\text{where } \mathcal{R}(n) = \frac{C\psi(n)}{1 - B\psi(n + 1)}X(n) \quad (3.45)$$

Equation (3.45) shows that

$$1 - B\psi(i) > 0 \quad (3.46)$$

Theorem 3.2 *For the strategy $u = u^*$ to pass the first two check points, the system parameters B, C and r must at least satisfy:*

$$rB < 1 \text{ and } C - B > 0 \quad (3.47)$$

To prove this, the fitness function representing the period two situation will be subjected to respectively the ESiS and CSS tests:

1. Check point 1:

$$1 = \mathcal{R}(1)\mathcal{R}(2) \quad (3.48)$$

$$= \left(\frac{C\psi(1)}{1 - B\psi(2)} \right) \left(\frac{C\psi(2)}{1 - B\psi(1)} \right) \quad (3.49)$$

$$= \left(\frac{C\psi(2)}{1 - B\psi(2)} \right) \left(\frac{C\psi(1)}{1 - B\psi(1)} \right) \quad (3.50)$$

$$= K(2)K(1) \quad (3.51)$$

$$\text{where } K(n) = \frac{C\psi(n)}{1 - B\psi(n)} \quad (3.52)$$

Defining K (not to be confused with \mathcal{K}) to take the place of \mathcal{R} has its advantages since

$$(K(n))_{u_R} = \frac{C}{(1 - B\psi(n))^2} (\psi(n))_{u_R} \quad (3.53)$$

Equation (3.51) can be used to define $\psi(1)$ in terms of $\psi(2)$ and eventually $(X(1))^u$ in terms of $(X(2))^u$ using (3.22) and $K(1)K(2) = 1$:

$$(X(1))^u = \frac{r}{\psi(1)} - 1 \quad (3.54)$$

$$\text{where } \psi(1) = \frac{1 - B\psi(2)}{(C^2 - B^2)\psi(2) + B} \quad (3.55)$$

The ESiS test further requires that $u = u^*$ must optimize the period two fitness function, so, using (6.45) and (3.53):

$$0 = (K(1)K(2))_{u_R} \quad (3.56)$$

$$= K(1)K(2) \sum_{i=1}^2 \frac{(K(i))_{u_R}}{K(i)} \quad (3.57)$$

$$= K(1)K(2) \left[\sum_{i=1}^2 \frac{1}{\psi(i)(1 - B\psi(i))} (\psi(i))_{u_R} \right] \quad (3.58)$$

$$= K(1)K(2) \sum_{i=1}^2 P(i) (\psi(i))_{u_R} \quad (3.59)$$

$$\text{where } P(n) = \frac{1}{\psi(n)(1 - B\psi(n))} \quad (3.60)$$

$$\text{with } (P(n))_{u_R} = -P^2(n)(1 - 2B\psi(n)) (\psi(n))_{u_R} \quad (3.61)$$

Since $K(1)K(2) = 1$, the optimization process (3.59) simplifies to:

$$P(1)(\psi(1))_{u_R} + P(2)(\psi(2))_{u_R} = 0 \quad (3.62)$$

Since from (3.70) $P(n) > 0$, the above can only be possible if the derivatives of $\psi(1)$ and $\psi(2)$ are opposite in sign. From (3.23), opposite signs can only result from, for instance, $X(1) > 1$ and $0 < X(2) < 1$ which will result in a negative $\ln X(2)$ and a positive $\ln X(1)$ making (3.62) possible. Further, if $0 < X(2) < 1$ then $0 < (X(2))^u < 1$ or, using (3.22), $0 < \frac{r}{\psi(2)} - 1 < 1$, showing that

$$\frac{r}{2} < \psi(2) < r \quad (3.63)$$

$$\text{similarly } 0 < \psi(1) < \frac{r}{2} \quad (3.64)$$

Therefore, if $X(1) > X(2)$, then $\psi(2) > \psi(1)$, which can also be seen from the definition of $\psi(n)$. Investigating which models are suited to a period two solution, requires further investigation:

From the relationship $X(1) = \mathcal{R}(2)X(2)$ it can be deduced that $\mathcal{R}(2) > 1$, similarly $X(2) = \mathcal{R}(1)X(1)$ implies that $\mathcal{R}(1) < 1$:

$$\mathcal{R}(1) < 1 \quad (3.65)$$

$$\frac{C\psi(1)}{1 - B\psi(2)} < 1 \quad (3.66)$$

$$C\psi(1) < 1 - B\psi(2) \quad (3.67)$$

and

$$1 < \mathcal{R}(2) \quad (3.68)$$

$$1 < \frac{C\psi(2)}{1 - B\psi(1)} \quad (3.69)$$

$$1 - B\psi(1) < C\psi(2) \quad (3.70)$$

$$(3.67) + (3.70)$$

$$(C - B)\psi(1) < (C - B)\psi(2) \quad (3.71)$$

If $(C - B) > 0$, then the above gives:

$$\psi(1) < \psi(2) \quad (3.72)$$

as it should be, but if $(C - B) < 0$ then the above gives $\psi(1) > \psi(2)$, which is not the case. Therefore (3.62) implies that for a period two ESiS to be possible, the system coefficients A_i must satisfy:

$$(C - B) > 0 \quad (3.73)$$

This of course also implies that $C^2 - B^2$ from equation (3.55) is positive.

2. Check point 2:

Taking the derivative of (3.59) and recalling that at $u = u^*$, $K(1)K(2) = 1$ and $(K(1)K(2))_{u_R} = 0$ and using (3.59):

$$(K(1)K(2))_{u_R u_R} = \left(K(1)K(2) \sum_{i=1}^2 P(i) (\psi(i))_{u_R} \right)_{u_R} \quad (3.74)$$

$$= \sum_{i=1}^2 \left((P(i))_{u_R} (\psi(i))_{u_R} + P(i) (\psi(i))_{u_R u_R} \right) \quad (3.75)$$

From equations (3.61) and (3.26):

$$(K(1)K(2))_{u_R u_R} = (rB - 1) \sum_{i=1}^2 \frac{P^2(i)\psi(i)}{r - \psi(i)} \left((\psi(i))_{u_R} \right)^2 \quad (3.76)$$

From (3.63) and (3.64), $r - \psi(n) > 0$, and since both the $\psi(n)$ and $P(n)$ are positive the above can only be negative if

$$rB < 1 \quad (3.77)$$

3.2.3 Model parameters conducive to a period three solution

Determining the expression for \mathcal{R} that describes a period three solution, we put

$$X(n - (3i - 1)) = X(1) \quad (3.78)$$

$$X(n - (3i - 2)) = X(2) \quad (3.79)$$

$$X(n - 3i) = X(3) \quad \forall i = 1, 2.. \quad (3.80)$$

with corresponding $\psi(1), \psi(2)$ and $\psi(3)$. Defining

$$D = \sum_{i=1}^{M/3} A_{3i-2} \quad (3.81)$$

$$E = \sum_{i=1}^{M/3} A_{3i-1} \quad (3.82)$$

$$F = \sum_{i=1}^{M/3} A_{3i}, \quad (3.83)$$

where $M = m$ if m is dividable by 3, $M = m + 1$ if $m + 1$ is dividable by 3 or $M = m + 2$ if $m + 2$ is dividable by 3. The difference equation (3.12) representing a

period three situation is then given by:

$$X(n) = \sum_{i=1}^m A_i \psi(n-i) X(n-i) \quad (3.84)$$

$$\begin{aligned} \text{specifically for } n = 3 \\ = D\psi(2)X(2) + E\psi(1)X(1) + F\psi(3)X(3) \end{aligned} \quad (3.85)$$

$$X(3)(1 - F\psi(3)) = D\psi(2)X(2) + E\psi(1)X(1) \quad (3.86)$$

The above equation shows in general that

$$X(n)(1 - F\psi(n)) = D\psi(n-1)X(n-1) + E\psi(n-2)X(n-2) \quad (3.87)$$

$$\text{where } 1 - F\psi(n) > 0 \quad (3.88)$$

Equation (3.88) must be true for all three $\psi(n)$ values in the range $[0, r]$ where r is in the range $[1, 2]$ which already shows that $F \ll 1$. A sufficient restriction on F will be that even in the worst case scenario when $\psi(n) = r$ that (3.88) will hold, that is:

$$Fr < 1 \quad (3.89)$$

Equation (3.14) now suggests that the fitness function representing the jump from $X(n-m)$ to $X(n)$ for (3.86) is given by:

$$X(3)(1 - F\psi(3)) = \left(D\psi(2) \frac{X(2)}{X(1)} + E\psi(1) \right) X(1) \quad (3.90)$$

but for purpose of defining a more manipulatable expression for $\mathcal{R}(n)$ the following regrouping is suggested:

$$X(3) \left((1 - F\psi(3)) - D\psi(2) \frac{X(2)}{X(3)} \right) = E\psi(1)X(1) \quad (3.91)$$

$$X(3) = \frac{E\psi(1)}{(1 - F\psi(3)) - D\psi(2) \frac{X(2)}{X(3)}} X(1) \quad (3.92)$$

$$= \mathcal{R}(1)X(1) \quad (3.93)$$

$$\text{where } \mathcal{R}(1) = \frac{E\psi(1)}{(1 - F\psi(3)) - D\psi(2) \frac{X(2)}{X(3)}} \quad (3.94)$$

In general:

$$X(n+2) = \mathcal{R}(n)X(n) \quad n = 1, 2, 3 \quad (3.95)$$

$$\text{where } \mathcal{R}(n) = \frac{E\psi(n)}{(1 - F\psi(n+2)) - D\psi(n+1) \frac{X(n+1)}{X(n+2)}} \quad (3.96)$$

Creating a fitness function that will not include X explicitly, $X(n+1)$ in the fraction $\frac{X(n+1)}{X(n+2)}$ in (3.96) is substituted with

$$X(n+1) = \frac{D\psi(n)X(n) + E\psi(n+2)X(n+2)}{1 - F\psi(n+1)} \quad (3.97)$$

from equation (3.87) which then simplifies (3.95) to an alternative version:

$$X(n+2) = \bar{\mathcal{R}}(n)X(n) \quad (3.98)$$

$$\text{where } \bar{\mathcal{R}}(n) = \frac{\psi(n)((D^2 - EF)\psi(n+1) + E)}{(1 - F\psi(n+2))(1 - F\psi(n+1)) - DE\psi(n+1)\psi(n+2)} \quad (3.99)$$

Since $\mathcal{R}(n)$ from (3.96) and $\bar{\mathcal{R}}(n)$ from (3.99) represent the same process, they can be equated to each other, resulting in a third more useful representation:

$$X(n+2) = \frac{E^2\psi(n) + D(1 - F\psi(n))}{D^2\psi(n+2) + E(1 - F\psi(n+2))}X(n) \quad (3.100)$$

$$= \frac{(E^2 - DF)\psi(n) + D}{(D^2 - EF)\psi(n+2) + E}X(n) \quad (3.101)$$

$$= \hat{\mathcal{R}}(n)X(n) \quad n = 1, 2, 3 \quad (3.102)$$

$$\text{where now } \hat{\mathcal{R}}(n) = \frac{(E^2 - DF)\psi(n) + D}{(D^2 - EF)\psi(n+2) + E} \quad (3.103)$$

Note from (3.88) that both parts of the fraction in equation (3.100) are positive implying that both parts of the fraction in equation (3.101) are also positive implying that if F is much smaller in value than both D and E then

$$E^2 - DF > 0 \quad (3.104)$$

$$D^2 - EF > 0 \quad (3.105)$$

Since the ESiS and CSS period three search will involve the product

$$\hat{\mathcal{R}}(1)\hat{\mathcal{R}}(2)\hat{\mathcal{R}}(3), \quad (3.106)$$

it will be useful to again define:

$$\hat{K}(n) = \frac{(E^2 - DF)\psi(n) + D}{(D^2 - EF)\psi(n) + E} \quad n = 1, 2, 3 \quad (3.107)$$

$$\text{with } \left(\hat{K}(n)\right)_{u_R} = \frac{(E^3 - D^3)(\psi(n))_{u_R}}{((D^2 - EF)\psi(n) + E)^2} \quad (3.108)$$

$$\text{and } \hat{\mathcal{R}}(1)\hat{\mathcal{R}}(2)\hat{\mathcal{R}}(3) = \hat{K}(1)\hat{K}(2)\hat{K}(3) \quad (3.109)$$

Theorem 3.3 For the strategy $u = u^*$ to pass the first two check points with system parameters D, E, F and r must at least satisfy:

$$Fr < 1, \quad (E^2 - DF) > 0, \quad (D^2 - EF) > 0 \quad (3.110)$$

as well as:

1. For the case $X(n) < 1$, $n = 1, 2$ and $X(3) > 1$:

$$E > D > F \quad (3.111)$$

with r range:

$$r < \frac{E - F}{D(E - D) + F(E - F)} \quad (3.112)$$

2. For the case $X(n) > 1$, $n = 1, 2$ and $X(n) < 1$, $n = 3$:

$$D > E > F \quad (3.113)$$

Since this event is less likely to produce a CSS for (3.110), it will not be extensively discussed.

To prove this, the fitness function representing the period three situation will be subjected to respectively the ESiS and CSS tests:

1. Check point 1:

$$\hat{K}(1)\hat{K}(2)\hat{K}(3) = 1 \quad (3.114)$$

This gives the equation

$$\prod_{i=1}^3 (1 - F\psi(i)) = (D^3 + E^3) \prod_{i=1}^3 \psi(i) + DE \sum_{i=1}^3 \psi(i)\psi(i+2)(1 - F\psi(i+1)) \quad (3.115)$$

The location of the optimum is where:

$$0 = \left(\hat{K}(1)\hat{K}(2)\hat{K}(3) \right)_{u_R} \quad (3.116)$$

$$= \hat{K}(1)\hat{K}(2)\hat{K}(3) \sum_{i=1}^3 \frac{\left(\hat{K}(i) \right)_{u_R}}{\hat{K}(i)} \quad (3.117)$$

$$= \sum_{i=1}^3 \frac{(E^3 - D^3) (\psi(i))_{u_R}}{\left((D^2 - EF)\psi(i) + E \right) \left((E^2 - DF)\psi(i) + D \right)} \quad (3.118)$$

$$= (E^3 - D^3) \sum_{i=1}^3 Q(i) (\psi(i))_{u_R} \quad (3.119)$$

where

$$Q(i) = \frac{1}{((D^2 - EF)\psi(i) + E)((E^2 - DF)\psi(i) + D)} \quad (3.120)$$

$$(Q(i))_{u_R} = -Q^2(i)T(i) (\psi(i))_{u_R} \quad (3.121)$$

$$T(i) = \frac{(D^2 - EF) \left((E^2 - DF)\psi(i) + D \right) + \left((D^2 - EF)\psi(i) + E \right) (E^2 - DF)}{\left((D^2 - EF)\psi(i) + E \right) (E^2 - DF)} \quad (3.122)$$

If the parameters

$$(E^2 - DF) > 0, \text{ and } (D^2 - EF) > 0 \quad (3.123)$$

then

$$\mathcal{R}(\hat{n}) > 0 \quad K(\hat{n}) > 0 \quad Q(n) > 0 \text{ and } T(n) > 0 \quad n = 1, 2, 3 \quad (3.124)$$

From (3.119) there can only be an optimum if at least one of the three terms is opposite in sign to the other two. The sign change can only come from the term $\ln X(i)$ in the derivative of $\psi(n)$ as explained in the period two case. Before more is said on this matter, the CSS test requires that:

2. Check point 2:

From (3.119), (3.114) and (3.121):

$$0 > \left(\hat{K}(1)\hat{K}(2)\hat{K}(3) \right)_{u_R u_R} \quad (3.125)$$

$$= (E^3 - D^3) \sum_{i=1}^3 \left(Q(i) (\psi(i))_{u_R} \right)_{u_R} \quad (3.126)$$

$$= (E^3 - D^3) \sum_{i=1}^3 \left(((Q(i))_{u_R} (\psi(i))_{u_R} + Q(i) (\psi(i))_{u_R u_R}) \right) \quad (3.127)$$

$$= (E^3 - D^3) \sum_{i=1}^3 \left(-Q^2(i)T(i) \left((\psi(i))_{u_R} \right)^2 + Q(i) (\psi(i))_{u_R u_R} \right) \quad (3.128)$$

$$= -(E^3 - D^3) \sum_{i=1}^3 W_1(i)W_2(i) \quad (3.129)$$

where

$$W_1(i) = \frac{Q^2(i) \left((\psi(i))_{u_R} \right)^2}{\psi(i)(r - \psi(i))} \quad (3.130)$$

$$\begin{aligned}
W_2(i) &= T(i)\psi(i)(r - \psi(i)) + \frac{2\psi(i) - r}{Q(i)} \\
&= \psi^2(i) \left(E(E^2 - DF) + D(D^2 - EF) + r(E^2 - DF)(D^2 - EF) \right) \\
&\quad + DE(2\psi(i) - r)
\end{aligned} \tag{3.131}$$

From (3.21) and (3.130), $(r - \psi(i)) > 0$ and $W_1(i)$ will always be positive. The first part of $W_2(i)$ is always positive for the choices (3.123) but the second part will only be positive if $2\psi(i) - r > 0$

If both $X(1)$ and $X(2)$ are less than 1 then $\psi(1)$ and $\psi(2)$ will have values between r and $\frac{r}{2}$ and the factor $(2\psi(n) - r) > 0, n = 1, 2$. The first two parts of (3.129) will therefore both be negative if $E > D$. The concern is with $X(3) > 1$ with a $\psi(3)$ value in the range $[0, \frac{r}{2}]$ which will result in $(2\psi(3) - r) < 0$ and will add one small positive contribution to (3.129):

$$-(E^3 - D^3)W_1(3) DE(2\psi(3) - r) \tag{3.132}$$

If $(2\psi(3) - r)$ is very small, that is,

$$\psi(3) \approx \frac{r}{2} \tag{3.133}$$

(implying that $X(3)$ is only slightly larger than one) the positive contribution will be negligible and the possibility of a CSS greater. If $D > E$ then both $X(1)$ and $X(2)$ will have to be larger than one while $X(3)$ will be smaller than one to improve the second derivative's slim (because the first parts of the $W_2(i)$'s will be positive) chance of being negative. A further interesting observation can be made from (3.99) on the matter of the likely locations of $X(1)$ and $X(2)$ with respect to each other. Since both $X(1)$ and $X(2)$ are taken as less than $X(3)$ in the case $E > D$, $\bar{\mathcal{R}}(1) > 1$ and $\bar{\mathcal{R}}(3) < 1$ or rather $-\bar{\mathcal{R}}(3) > -1$ then from (3.98):

$$\psi(1) \left((D^2 - EF)\psi(2) + E \right) > (1 - F\psi(2))(1 - F\psi(2)) - DE\psi(2)\psi(3) \tag{3.134}$$

$$-\psi(3) \left((D^2 - EF)\psi(1) + E \right) > -(1 - F\psi(2))(1 - F\psi(1)) + DE\psi(1)\psi(2) \tag{3.135}$$

$$(3.134) + (3.135) \tag{3.136}$$

$$\frac{\psi(3)}{\psi(1)} < \frac{E - F - \psi(2)(DE - F^2) + \psi(2)(D^2 - EF)}{E - F - \psi(2)(DE - F^2) + \psi(1)(D^2 - EF)} \tag{3.137}$$

Equation (3.137) was derived with the assumption that both parts of the fraction on the right are positive:

$$E - F - \psi(2)(DE - F^2) + \psi(2)(D^2 - EF) > 0 \quad (3.138)$$

$$E + \psi(2)(D^2 - EF) > F + \psi(2)(DE - F^2) \quad (3.139)$$

$$\text{and } E - F - \psi(2)(DE - F^2) + \psi(1)(D^2 - EF) > 0 \quad (3.140)$$

$$E + \psi(1)(D^2 - EF) > F + \psi(2)(DE - F^2) \quad (3.141)$$

The left hand side of (3.137) is less than one, which, in the worst case scenario when $\psi(3) \in [0, \frac{r}{2}]$ is at its largest and $\psi(1) \in [\frac{r}{2}, r]$ is at its smallest can also be very close to 1. This limits the right hand side to values greater than one ($\psi(2) > \psi(1)$) or equals to one ($\psi(2) = \psi(1)$). If the latter is true, using $\hat{\mathcal{R}}(n)$ from (3.103), $\hat{\mathcal{R}}(2) = 1$ which solves for $\psi(1) = \psi(2)$:

$$\psi(1) = \psi(2) = \frac{1}{D + E + F} \quad (3.142)$$

Equation (3.114) then shows that

$$\psi(3) = \frac{1}{D + E + F} \quad (3.143)$$

which is clearly not a period three solution but a fixed point and will not optimize (3.106). This option can therefore be excluded leaving ($\psi(2) > \psi(1)$) as the more likely occurrence and implying that $X(2) < X(1) < X(3)$. On the matter of (3.139) and (3.141) being true, even in the worst case scenario when $\psi(1)$ is at its lower boundary $\frac{r}{2}$ and $\psi(2)$ at its upper boundary r in (3.141), shows that the restriction on r values for the proposed period three solution described by the system coefficients (3.110) and (3.111) is:

$$r < \frac{E - F}{D(E - D) + F(E - F)} \quad (3.144)$$

Investigating the system requirements for the possible existence of a chaotic periodic point, will be based on the theorem *Period three implies Chaos* from Li and Yorke which is briefly discussed in Appendix 1 [67]. The theorem is applicable to all continuous functions $F : R \rightarrow R$ and states that if F has a periodic point of prime period three, then F can have periodic points of all other periods as well, including chaos. Another periodic state of interest is quasi periodicity and will be discussed next.

3.3 Quasi periodic Solutions

In signal processing, a quasi periodic signal is a waveform where adjacent cycles' lengths are almost identical but not exactly [14, 12]. The overall impression of such a waveform is one of periodicity but when comparing periods, they do not match on a microscopic scale, that is, for a cycle of length w ,

$$|X(n+w) - X(n)| < \varepsilon \quad (3.145)$$

A perfectly periodic function with period w is one such that

$$|X(n+w) - X(n)| = 0 \quad (3.146)$$

Periodic functions can be simulated with an infinite sum of sine and cosine functions on account of their own periodicity. Such a representation is called a Fourier series where, for the discrete case where one period is described by N points, $X(n)$ can alternatively be written as [114]:

$$\begin{aligned} X(n) &= \frac{1}{N} \sum_{k=0}^{N-1} c_k e^{\frac{i2\pi nk}{N}}, \quad X(n+N) = X(n) \\ &= \frac{c_0}{N} + f(n) \end{aligned} \quad (3.147)$$

$$\text{where } f(n) = \frac{1}{N} \sum_{k=1}^{N-1} c_k e^{\frac{i2\pi nk}{N}} \quad (3.148)$$

It will be assumed that for very long periods (large N), $f(n)$ is a rapid converging function, that is, $|f(n)| \ll 1$ implying that in the calculations to follow $(f(n))^m$ will be taken as negligible for $m > 1$. The calculations will also be limited to quasi periodic patterns in populations that do not deviate very far from being periodic. The discrete representation of c_k is

$$c_k = \sum_{n=0}^{N-1} X(n) e^{\frac{-i2\pi nk}{N}} \quad (3.149)$$

$$\text{where } c_0 = \sum_{n=0}^{N-1} X(n) \quad (3.150)$$

Which means that the first term in (3.147) is the average value $X(n)$ has over the interval $[0, N-1]$ which is approximately one as the oscillations expected in a quasi periodic situation will be around the carrying capacity of the habitat which has been

scaled to one. Therefore:

$$\begin{aligned}
X(n) &\approx 1 + f(n) & (3.151) \\
\text{and } \psi(n) &= \frac{r}{1 + (X(n))^u} \\
&\approx \frac{r}{1 + (1 + f(n))^u} \\
&\approx \frac{r}{1 + (1 + uf(n))} \quad (\text{binomial expansion}) \\
&= \left(\frac{r}{u}\right) \frac{1}{\frac{2}{u} + f(n)} \\
&= \left(\frac{r}{u}\right) \left(\frac{u}{2} - \frac{u^2}{4}f(n)\right) \\
&= \frac{r}{2} - \frac{ru}{4}f(n) \\
\text{so that } \psi(n)X(n) &\approx \frac{r}{2} \left(1 + \frac{2-u}{2}f(n)\right) & (3.152)
\end{aligned}$$

Note that since $X(n) > 0$, $f(n) > -1$. Equations (3.151) and (3.152) are then used to replace $X(n)$ and $\psi(n)$ in (3.12):

$$\begin{aligned}
X(n) &= \sum_{i=1}^m A_i \psi(n-i) X(n-i) \\
1 + f(n) &\approx \sum_{i=1}^m A_i \frac{r}{2} \left(1 + \frac{2-u}{2}f(n-i)\right) \\
&= \frac{r}{2} \sum_{i=1}^m A_i + \frac{r(2-u)}{4} \sum_{i=1}^m A_i f(n-i) \\
&= \frac{r}{2} A + \frac{r(2-u)}{4} \sum_{i=1}^m A_i f(n-i) & (3.153)
\end{aligned}$$

$$\text{where } A = \sum_{i=1}^m A_i \quad (3.154)$$

Since (3.153) must be valid for all n it follows that

$$1 \approx \frac{r}{2} A \quad \text{or} \quad rA \approx 2 \quad (3.155)$$

$$f(n) \approx \frac{r(2-u)}{4} \sum_{i=1}^m A_i f(n-i) \quad \forall n \quad (3.156)$$

$$= \left(\frac{r(2-u)}{4} \sum_{i=1}^m A_i \frac{f(n-i)}{f(n-m)}\right) f(n-m) \quad (3.157)$$

$$= R_f(u, \bar{f}(n-i))f(n-m) \quad (3.158)$$

$$\text{where } R_f(u, \bar{f}(n-i)) = \frac{r(2-u)}{4} \sum_{i=1}^m A_i \frac{f(n-i)}{f(n-m)} \quad (3.159)$$

$$\bar{f}(n-i) = [f(n-1), f(n-2), \dots, f(n-m)] \quad (3.160)$$

The optimal u will ensure small oscillations around one, therefore, $f(n)$ will oscillate around zero, taking on negative and positive values. The useful result here is that wave form solutions, or alternatively, solutions with very long periods (or quasi periodic with $\varepsilon \ll 1$) can be expected for the age-structured model if, using (3.155),

$$rA \approx 2 \quad (3.161)$$

3.4 Useful results from Chapter 3

1. The difference equation and fitness function for the age-structured population model with a Shepherd recruitment function is given by

$$X(n) = \sum_{i=1}^m A_i \psi(n-i) X(n-i) \quad (3.162)$$

$$= \left(\sum_{i=1}^m A_i \psi(n-i) \frac{X(n-i)}{X(n-m)} \right) X(n-m) \quad (3.163)$$

$$= \mathcal{R}(u, \bar{X}(u)) X(n-m) \quad (3.164)$$

$$\text{where } A_i = b_i L_{i-1} \quad (3.165)$$

$$\psi(n) = \frac{r}{1 + (X(n))^{u(n)}} \quad (3.166)$$

$$\bar{X} = [X(n-1), X(n-2), \dots, X(n-m)] \quad (3.167)$$

Although there are other options for defining \mathcal{R} , this version faithfully delivers an optimum if it exists. To make a first next prediction on the state of $X(n)$ one requires m initial values. Instead of calculating the fitness function \mathcal{R} directly, it will be easier to rather calculate the ratio

$$\mathcal{R}(u, \bar{X}(u)) = \frac{X(n)}{X(n-m)} \quad (3.168)$$

2. For the non age-structured case, $A_1 = b_1 s_0 = 1$ will be the only non zero coefficient of (3.14).
3. Table 3.1 summarizes the combinations of the system coefficients that can predict the periodicity of an age-structured model.

PERIODIC PREDICTORS

	Symbols
	$A = \sum_{i=1}^m A_i$ $B = \sum_{i=1}^{m/2} A_{2i}$ $C = \sum_{i=1}^{m/2} A_{2i-1}$ $D = \sum_{i=1}^{m/3} A_{3i-2}$ $E = \sum_{i=1}^{m/3} A_{3i-1}$ $F = \sum_{i=1}^{m/3} A_{3i}$
Period	Coefficient requirements
1	no fixed point possibility
2	$rB < 1$ $(C - B) > 0$
3	$rF < 1$ $(E^2 - DF) > 0$, $(D^2 - EF) > 0$ $E > D > F$ for $X(1), X(2) < 1$ and $X(3) > 1$ with $r < \frac{E-F}{D(E-D)+F(E-F)}$ or $D > E > F$ then $X(1), X(2) > 1$ and $X(3) < 1$
quasi	$rA \approx 2$

Table 3.1: Combinations of the age-structured system coefficients predicting certain periodic outcomes.

“What’s happening out there?”

“Shall I describe it to you? Or would you like me to find you a box?” - Lord of the Rings, J.R.R. Tolkien

Chapter 4

The Optimizing Algorithm

From the AD analysis in Chapter 2 it was seen that determining the ESS strategy involves determining for which u the \mathfrak{R} function reaches a maximum along the u_R axes of established residents and a minimum along the u_M axes of initially small numbered challengers in the competition model. It is from this knowledge that the optimization method used must be able to take advantage of the gradient aspect involved in the search and make a next prediction based on the sign of \mathfrak{R} 's local fitness gradient with respect to the two directions u_R and u_M . For an initial choice of u , say u_o , the local fitness gradient of \mathfrak{R} in the u_R direction is:

$$(\mathfrak{R})_{u_R}^o = (\mathcal{R})_{u_R}^o \quad (4.1)$$

$$= \frac{\mathcal{R}(u_o + h, X_o) - \mathcal{R}(u_o - h, X_o)}{2h} \quad (4.2)$$

where $()^o$ is where \mathfrak{R} and \mathcal{R} are evaluated at $u_M = u_R = u_o$. Differentiating \mathfrak{R} along the u_R axes gives the same result as differentiating \mathcal{R} along the u_R axes and will be approximated using the central difference formula as shown in (4.2).

If the central difference formula is used to approximate the derivative, the equilibrium population X_o in \mathcal{R} is exposed to slightly different strategies $u_o + h$ and $u_o - h$. The better of these two strategies will cause the bigger (positive) fitness in \mathcal{R} and will show the direction of even better strategies. Alternatively, seeking a minimum for \mathcal{M} will involve calculating populations X_{-h} and X_{+h} at strategies $u_o - h$ and $u_o + h$ respectively and exposing these populations to the strategy u_o :

$$(\mathfrak{R})_{X_M}^o = (\mathcal{M})_{X_M}^o \quad (4.3)$$

$$= \frac{\mathcal{M}(u_o, X_{+h}) - \mathcal{M}(u_o, X_{-h})}{2h} \quad (4.4)$$

Differentiating \mathfrak{R} along the u_M axes will give the same results as differentiating \mathcal{M} along the u_M axes. The next better choice is then in the opposite direction of the

strategy of the population that reacted to the exposure to u_o with the larger positive fitness in \mathcal{M} .

The algorithm formulated in this chapter will be based on the optimization of \mathcal{R} . The search process will focus on check points 1 and 2 of the ESS criteria formulated in Chapter 2. If an optimal strategy exists along this path, it will be a CSS as well as an EStS. Determining whether this u_o is also a NIS will be done by evolving neighborhood populations with strategies slightly different from u_o and then switching strategies with u_o and recording or plotting the initial response to this switch. If a strategy tests CSS only, it will be indicated as u_R and if it tests NIS as well, it will be shown as the ESS strategy u^* .

4.1 The Search Algorithm

Extending the above to the difference equation (3.12), the population $\bar{X}_o(u_o)$ must be evolved from a given initial population \bar{X}_I after which we will define:

$$\mathcal{R}(u_o, \bar{X}(u_o)) = \frac{X(n)}{X(n-m)} \quad (4.5)$$

the resident (steady) population \bar{X}_o will then be exposed to alternative strategies $u_o + h$ and $u_o - h$ where ($h \approx 0.01$) through two independent strategy switches in \mathcal{R} for the period chosen¹. A positive gradient inspires a next choice for u_o to be to the right of u_o , say at $u_o = u_o + f$ where initially $f = 1$ to speed up the search. The iteration of (3.12) is repeated with \bar{X}_I and the new u_o which will result in a new resident \bar{X}_o . This process is repeated until a strategy u_o is reached for which the gradient tests negative. Implying that the next best strategy is now to the left of the current u_o but still to the right of the previous strategy. Choosing the next u_o will have to be in smaller steps, say $f = \frac{f}{10}$ and in the opposite direction, that is, $u_o = u_o - f$. For as long as the gradient tests negative u_o will be decreased by another f until the fitness gradient changes sign again in which case f is again rescaled $f = \frac{f}{10}$ and u_o is adjusted to the right by this amount. This process repeats until the fitness gradient for u_o (4.2) tests desirably close to zero. Such a strategy represents an EStS for the model. To establish if this u_o is also a NIS, populations at equilibrium states with strategy values in a neighborhood of u_o must be subjected to u_o and their initial responses over one period monitored. Two such populations either side of u_o will be considered in the algorithm using strategies slightly bigger and smaller than u_o . If both show a positive growth rate as a result of the switch, then $u_o = u^*$ is also a NIS and therefore passes all three check points. Two points need to be considered in the

¹This choice will be discussed later.

programming, namely the inclusion of a variety of periods and secondly, an optional subroutine for the competition model between the player playing the ESS strategy and nearby competitors:

1. The invasion exponent:

To include a wide variety of possible types of equilibria, such as periodic, quasi periodic and chaotic stable equilibria it will be useful to rather use the invasion exponent I as defined in (2.4) as the fitness proxy instead of the \mathcal{R} product representing the equilibrium as it will lead to similar conclusions but is better equipped to deal with large periods [84, 85, 84]. The prerequisites for $u = u^*$ to represent an EStS for the invasion exponent I is then:

$$\text{ESiS: } I \Big|_{u=u^*} = 0 \quad (4.6)$$

$$(I)_{u_R}^* = 0 \quad (4.7)$$

$$\text{CSS: } (I)_{u_R u_R}^* < 0 \quad (4.8)$$

2. The pairwise invasibility plots (PIPs):

Extending (2.15) and (2.16) to the age structured case, the competition model between \bar{X}_R playing u_R and another population \bar{X}_M playing u_M has configuration:

$$X_R(n) = \mathcal{R}(u_R, \bar{X}_R + \bar{X}_M)X_R(n-m) \quad (4.9)$$

$$X_M(n) = \mathcal{M}(u_M, \bar{X}_M + \bar{X}_R)X_M(n-m) \quad (4.10)$$

Iteration of the competition model pair (4.10) and (4.9) and recording the survival outcomes after several combination of u_R and u_M , gives the pairwise invasibility plots or PIPs that show the stability properties of the strategy combinations. The competition model is run over 40000 cycles and the population output is taken as the average of the particular population over the last 10000 or so cycles. The algorithm as well as more detail will be given in Chapter 5.

4.2 The Gradient Search Program

Unlike *The Grinch* from the tale of Dr. Seuss², who solved world hunger at exactly five o'clock but told no one, the algorithm used in calculating the results in the next section is discussed in full detail here:

²From the movie: "How the Grinch Stole Christmas"

1. Input:

$z7 = input$	carrying capacity K of habitat
$m = input$	the amount of age classes excluding juvenile
$b = input$	vector with birth rates : $[b_1 b_2 .. b_m]$
$s0 = input$	infant survival to age 1
$s = input$	survival rates : $[s_1 s_2 .. s_{m-1}]$
$r = input$	population growth rate when densities are small
$u = input$	first choice of u_o
$h = 0.01$	step size for the difference equation
$f = 1$	initial adjustment to u_o for next choice of u
$M = input$	number of times (3.12) must be iterated with every new u_o
$N = input$	period of periodic point tested for ESS
$in = input$	value for $X_{initial}$
$TH = input$	desired accuracy (threshold) with respect to zero

2. Routine 1: calculating the coefficients $A(i)$ of $X(n - i)$:

```

for i = 1 : m
    S = s0
    if i > 1
        for j = 1 : i - 1
            S = S * s(j)
        end
    end
    A(i) = b(i) * S
end

```

3. Routine 2: (Check points 1 and 2 as discussed in Chapter 2) X is the population iterated at u_o and $X1$ and $X2$ are what happens to X after a strategy switch with, respectively, strategy values slightly smaller and larger than u_o . The three difference equations for each of X , $X1$ and $X2$ are calculated as follows:(a) The difference equation requires m initial values for $X, X1, X2$

```

for i = 1 : m

```



```

X(i) = in
X1(i) = in
X2(i) = in
end

```

- (b) Switch X strategy u with slightly bigger $u1 = u + h$ and slightly smaller $u2 = u - h$:

```

for i = 1 : M
  for ii = i : i + (m - 1)
    psi(ii) = r / (1 + (X(ii) / z7)^u)    calculating  $\psi$  at original  $u_o$ 
    psi1(ii) = r / (1 + (X(ii) / z7)^u1)   $\psi$  at bigger  $u1$ 
    psi2(ii) = r / (1 + (X(ii) / z7)^u2)   $\psi$  at smaller  $u2$ 
    P(ii) = psi(ii) * X(ii)
    P1(ii) = psi1(ii) * X1(ii)
    P2(ii) = psi2(ii) * X2(ii)
  end
end

```

- (c) Building the difference equations:

```

x = 0    initiate difference equation
x1 = 0
x2 = 0

for j = 1 : m
  x = x + A(j) * P(i + m - j)
  x1 = x1 + A(j) * P1(i + m - j)
  x2 = x2 + A(j) * P2(i + m - j)
end

X(i + m) = x     $X_i$  calculated at  $u_o$ 
X1(i + m) = x1  the changed  $X(u1)$ 
X2(i + m) = x2  the changed  $X(u2)$ 
end

```

- (d) Calculating the invasion exponents for X , $X1$ and $X2$ using population ratios to express \mathcal{R} :

```

SI = 0    initiate invasion exponent

```

```

                SI1 = 0
                SI2 = 0
                for j = M - (N - 1) : M
                    logR(j) = log(X(j + m)/X(j))
                    SI = SI + logR(j)
                logR1(j) = log(X1(j + m)/X1(j))
                    SI1 = SI1 + logR1(j)
                logR2(j) = log(X2(j + m)/X2(j))
                    SI2 = SI2 + logR2(j)
                end
                IX = [SI2/N SI/N SI1/N]    I values on  $u_o$  axes    (4.11)

```

(e) Calculating the slope of the invasion exponent I on u_o axes:

```

                der = (IX(3) - IX(1))/(2 * h)    gradient of  $I$  at  $u_o$ 
                DER = (IX(3) - 2 * IX(2) + IX(1))/(h * h)    second derivative of  $I$  at  $u_o$ 
                ss(t) = sign(der)    the sign of  $der$ 
                if |der| < TH and |I| < TH and DER < 0    CSS maximum
                    display :  $u_o$  is a CSS

```

4. Routine 3: (check point 3 from Chapter 2) for populations XX iterated at strategies z close to u_o , calculate the effect of subjecting XX to u_o .

(a) Calculate XX in the absence of X at neighborhood values (z) either side of u_o :

```

                k = 0    initiate counter for  $I$  vector on  $u_M$  axes
                for z = u1 and z = u2    values to the left and right of  $u_o$ 
                    for i = 1 : m
                        XX(i) = in    neighborhood  $XX$  using strategy  $z$ 
                    end
                    for i = 1 : M
                        for ii = i : i + (m - 1)
                            psiX(ii) = r/(1 + (XX(ii)/z7)^z)     $\psi$ for original  $XX$ 
                            PX(ii) = psiX(ii) * XX(ii)
                        end

```

```

                 $xx = 0$ 
                for  $j = 1 : m$ 
 $xx = xx + A(j) * PX(i + m - j)$ 
                end
 $XX(i + m) = xx$      $XX$  population in absence of  $u_o$ 
                end

```

(b) The change in XX as a result of a strategy switch with u_o :

```

                 $YY(i) = in$     change in  $XX$  when exposed to  $u_o$ 
                for  $i = 1 : M$ 
                for  $ii = i : i + (m - 1)$ 
 $psiY(ii) = r / (1 + (XX(ii) / z7)^u)$     expose  $XX$  to  $u_o$ 
                 $PY(ii) = psiY(ii) * YY(ii)$ 
                end
                 $yy = 0$ 
                for  $j = 1 : m$ 
 $yy = yy + A(j) * PY(i + m - j)$ 
                end
 $YY(i + m) = yy$     changed  $XX$  as a result of strategy switch
                end

```

(c) Calculate the invasion exponents of changed populations YY using population ratio to express \mathcal{M} :

```

                 $SY = 0$ 
                for  $j = M - (N - 1) : M$ 
 $logRY(j) = log(YY(j + m) / YY(j))$ 
                 $SY = SY + logRY(j)$ 
                end
                 $k = k + 1$ 
 $IY(k) = SY / N$      $I$  for  $\mathcal{M}$  on  $u_M$  axes (4.12)
                end

```

(d) Calculating the slope of the invasion exponent I on the u_M axes

```

 $deriv = (IY(2) - IY(1)) / (2 * h)$     first derivative of  $I$  at  $u_o$ 

```

```

DERV = (IY(2) - 2 * IX(2) + IY(1))/(h * h)    second derivative of IY at  $u_o$ 
    if abs(der) < TH and DERV > 0    NIS minimum
        display :  $u_o$  is a NIS
    end

```

5. Adjustment for the next best u_o : If u_o is both a CSS and a NIS then it is the champion strategy u^* and the program must be terminated. If not, then it is time to make a next best choice for u_o based on the sign of *der*:

if this is the first run, there will not be a previous derivative to compare this derivative with to establish if there's been a change in sign and the status quo is held, *f* unchanged, otherwise:

```

    if ss(t) ≠ ss(t - 1)    if slope has changed sign, optimum lies between
        f = f/10    reduce step size
    end
    if der < 0
        u = u - f    reverse
    end
    if der > 0
        u = u + f    reverse
    end
    if f < 0.00001
        break    buffer for no further convergence towards ESS
    end
    if u < 0 or u = 0
        break    when there is no ESS
    end

```

(4.13)

After a suitable choice for *f* has been made, the program returns to routine 1.

4.2.1 Algorithm alternatives and short cuts

1. To minimize iteration time: for very long periods or unpredictable periods, the above process can be made part of an approximation algorithm. For a fixed number of preliminary iterations, say $M = 60000$, the optimization must be done for $N = 8! = 40320$ which is inclusive of all usually expected periods and is big enough to indicate the possibility of quasi and chaotic situations as well.

2. Testing for different values of r : The above program can be run for r ranging from say 1.0 until 2.0 in steps of a chosen size, recording its findings at these respective r values.
3. Routine 3 can be made into a subroutine of routine 2 cutting down on run time as u_o must first be a CSS and if it already fails this test, there is no need to test for a NIS and the program must return to routine 1 where the new $u_o = u_o + f$ is based on the sign of der .
4. To establish the period of the output u^* , run the following subroutine after u passes both the CSS and NIS tests:

```

      for p = 1 : M - (s + 1)
      C1 = |X(M)/X(M - p) - 1|
      Cs = |X(M - s)/X(M - s - p) - 1|   s point confirms cycle repetition
      if C1 < TH and Cs < TH
          the period is : p
          break
      end
      end

```

5. If $f < 0.0001$ then choose u_o to be the mid value between the current and the previous value where der changed sign. Test for CSS and NIS and if these tests are negative terminate search for this r value.
6. For data already calibrated according to the carrying capacity K , the value $z7=1$.
7. DER and $DERV$ can be replaced with

$$IX(2) > \max(IX(1), IX(3)) \quad (4.14)$$

$$\text{and } IX(2) < \min(IY(1), IY(3)) \quad (4.15)$$

respectively.

8. X is the recruitment population, if the population as a whole needs to be calculated, then routine one should additionally to $A(i)$ which calculates the coefficient combination $b_i L_{i-1}$, calculate only the combination (without b_i) L_{i-1} in $x_i = L_{i-1} \psi(n - i) X(n - i)$ for $i = 1, \dots, n$. That is:

$$\bar{A}(i) = S \quad (4.16)$$

In subroutine two, when putting the difference equation together, the adult population total $\sum_{i=1}^m x_i$ then comes from adding together

$$xt = xt + \bar{A}(j) * P(i + m - j) \quad (4.17)$$

The population total at time i is then:

$$XT(i + m) = X + xt \quad (4.18)$$

9. For chaotic periods both the NIS and CSS tests might not be reliable once u^* has been established as the data can be scattered unfavorably about u^* . In these cases a visual test is suggested which involves calculating IX from equation (4.11) in routine 2 over a wider range about u^* and not just at $u1$ and $u2$. Similarly, $IY(k)$ from equation (4.12) in routine 3 can be plotted over a wider range of k values about u^* . The plots will show if all the IX and IY values are respectively scattered strictly below (CSS) and above (NIS). Examples of such plots are shown in Figures 5.2 till 5.5 in Chapter 5 and discussed in more detail in section 5.1.

4.3 Algorithm Points Worth Remembering

1. To include a wide variety of possible types of equilibria, such as periodic, quasi periodic and chaotic stable equilibria it will be useful to rather use the average of the log of the product of the \mathcal{R} 's describing the period under investigation as opposed to the direct product describing a specific period itself. This version of the periodic progress is called the invasion exponent I and takes the form [105]:

$$I = \frac{1}{N} (\log |\mathcal{R}_1| + \dots + \log |\mathcal{R}_N|) \quad (4.19)$$

The prerequisites for u^* to be an ESS now translates into: An ESS strategy $u = u^*$ of the periodic combination

$$\prod_{i=1}^N \mathcal{R}_i = 1 \quad (4.20)$$

is also an ESS strategy of I if at $u = u^*$

$$I = 0 \quad (4.21)$$

$$(I)_u = 0 \quad (4.22)$$

$$(I)_{uu} < 0 \quad (4.23)$$

2. To cut down on iteration time: for very long periods or unpredictable periods, the above process can be made part of an approximation algorithm. For a fixed amount of preliminary iterations, say $M = 60000$, the optimization must be done for $N = 8! = 40320$ which is inclusive of all usually expected periods and is big enough to indicate the possibility of quasi and chaotic situations as well.
3. It will be seen in the gallery of Chapter 5 that the iteration amounts M and N affect the smoothness of the \mathcal{M} graph in chaotic cases. A combination of very large M and N values might very well converge to a smooth curve.
4. There will probably not be ESS strategies for all choices of r . To establish for which r 's there will be u^* 's, routine 1 till 3 can be incorporated into a loop where r can cover a desired range, for example

for $r = 1 : 0.01 : 2$,

and then record the ESS outcomes.

"A wizard is never late. Nor is he early. He arrives precisely when he means to"
- Lord of the Rings, J.R.R. Tolkien

Chapter 5

The Gallery

The ESS outcomes of different age-structured hypothetical cases and one real world case will be investigated in this section. The reliability of the periodic predictions based on the system coefficients A_i as discussed in Chapter 3 in Table 3.1 will be tested here. The real world case will necessitate a time dependent coefficient as \mathcal{K} , b_i and s_i are not constant in the real world, but fluctuate with environmental conditions. Without such a feature, the algorithm generated population cannot match the real population and nothing can be gained from this exercise. Fortunately, incorporating a time dependent variable will only change one statement in the algorithm of Chapter 4.

5.1 Preliminary Discussions

1. Three hypothetical cases:

- (a) One age group: This corresponds to the model description (3.14) where $A_1 = 1$ is the only non zero coefficient and the difference equation will trim down to

$$X(n+1) = \psi(n)X(n)$$

From Table 3.1 in Chapter 3,

$$A = D = C = 1 \tag{5.1}$$

$$B = E = F = 0 \tag{5.2}$$

Which indicates strong period two possibilities as well as probable quasi periodicity for $rA \approx 2$.

- (b) Two age groups: For the hypothetical choices $s_0 = 0.2$, $s_1 = 0.7$ and $b_1 = 2$, $b_2 = 4$,

$$A = 0.96, \quad B = 0.56, \quad C = 0.4 \quad (5.3)$$

$$D = 0.4, \quad E = 0.56, \quad F = 0 \quad (5.4)$$

Clearly the second period test $C - B > 0$ does not apply but the period three test will apply. Quasi periodic cycles, if any, can be expected around $r \approx 2.1$.

- (c) Three age groups: For the hypothetical choices $s_0 = 0.25$, $s_1 = 0.6$, $s_2 = 0.7$ and $b_1 = 1.5$, $b_2 = 2$, $b_3 = 4$,

$$A = 1.095, \quad B = 0.3, \quad C = 0.795 \quad (5.5)$$

$$D = 0.375, \quad E = 0.3, \quad F = 0.42 \quad (5.6)$$

This choice will not pass the period three test, but will pass the period 2 test provided $r < \frac{1}{B} = 3$. Quasi periodic cycles, if any, can be expected when $r \approx 1.8$.

2. The plots:

- (a) The growth rate plots:

- i. The optimization algorithm in Chapter 4 was made the body of a loop where r ranged from the value 1.00 to the value 2.00 in steps of 0.02 and the CSS and NIS strategy outcomes were recorded separately.
- ii. The threshold value TH in the algorithm was taken as 0.001 which proved to be desirably close enough to zero without compromising accuracy of the optimization process.
- iii. The carrying capacity was taken as $\mathcal{K} = 1$ which resulted in population outcomes arranged about the value 1. When real life data is used to compare the accuracy of the population prediction, it must therefore also be scaled accordingly. This will be shown for the Pacific sardine population in section 5.4.
- iv. For illustrational purposes, a few significant strategies were chosen to illustrate CSS, NIS, ESS and other interesting phenomena graphically. Once the algorithm from Chapter 4 terminated with an optimal u_o on the u_R axes, routine 2 (up to equation (4.11)) was incorporated into a loop where X_o is exposed to more neighborhood strategies in the range (for example) $u_i = u_o - 0.5 : 0.01 : u_o + 0.5$, plotting the $IX(i)$'s generated in (4.11) against u_i . This is the CSS plot (\mathcal{R}) and is shown

as the black graph in the growth rate plots in Figures 5.2 till 5.5. Similarly, routine 3 (up to equation (4.12)) was incorporated into a loop where neighborhood populations XX_i can be generated at the neighborhood strategies $z_i = u_o - 0.5 : 0.01 : u_o + 0.5$. Each of the generated XX_i 's are then exposed to u_o , and the $IY(i)$'s in (4.12) so generated are then plotted against the z_i . This is the NIS graph (\mathcal{M}) and is coloured blue in the growth rate plots. If a certain strategy is both a minimum point for the blue graph and a maximum point for the black graph then this strategy is an ESS.

(b) The pairwise invasibility plots (PIPs):

A PIP plot is a graphical representation of the outcomes of the competition model between an established residential population X practicing strategy u_R and an initially small challenger population x practicing strategy u_M . The PIPs in this chapter are specifically designed to show the outcomes of different strategy combinations for the established X on the horizontal axes and the initially small x on the vertical axes in a neighborhood of the algorithm generated strategy u_o . This approach deviated slightly from the PIP plots defined in [37, 84] where the plots represent combination where x invades X . This provides a colourful visual representation of the invasibility properties of the CSS, ESS and the Garden of Eden strategies. The best way to explain how the competition model as discussed in Chapter 2 works is to show the algorithm. For the two age group case with initial values of 0.8¹ for the resident X and 0.01 for the initially small challenger x , the algorithm representing the competition between these two populations across a grid of strategy values centered at u_o is given by:

i. Initiate u_M, u_R grid about u_o :

$$\text{for } uR = u0 - 0.5 : 0.01 : u0 + 0.5$$

$$\text{for } uM = u0 - 0.5 : 0.01 : u0 + 0.5$$

ii. Calculate populations starting with an established resident with population size near $\mathcal{K} = 1$ and that of the challenger near zero:

$$X(2) = 0.8;$$

$$X(1) = 0.8;$$

$$x(1) = 0.01;$$

$$x(2) = 0.01;$$

¹A value close to the carrying capacity of 1.

```

                                for i = 1 : M
      psiR(i) = r/(1 + (X(i) + x(i))uR);    from (4.9)
      psiR(i + 1) = r/(1 + (X(i + 1) + x(i + 1))uR);
      X(i + 2) = A(1) * psiR(i + 1) * X(i + 1)    change in resident
                + A(2) * psiR(i) * X(i);
      psiM(i) = r/(1 + (X(i) + x(i))uM);    from (4.10)
      psiM(i + 1) = r/(1 + (X(i + 1) + x(i + 1))uM);
      x(i + 2) = A(1) * psiM(i + 1) * x(i + 1)    change in challenger
                + A(2) * psiM(i) * x(i);
                                end

```

iii. Calculate the average population size over the last 10×10^3 iterations:

```

      Xav = (sum(X(M - 9999 : M)))/10000;
      xav = (sum(x(M - 9999 : M)))/10000;

```

iv. Compare populations:

```

      if Xav > xav    and    xav < 0.01
      plot(uR, uM, 'black')    X resident+eliminates x
      end
      if xav > Xav    and    Xav < 0.01
      plot(uR, uM, 'blue')    x resident + eliminates X
      end
      if Xav > xav    and    xav > 0.01
      plot(uR, uM, 'red')    X resident + co exists with x
      end
      if xav > Xav    and    Xav > 0.01
      plot(uR, uM, 'green')    x resident + co exists with X
      end
      if abs(Xav - xav) < 0.001
      plot(uR, uM, 'black*')    tying strategies x = X
      end

```

v. End evaluation at current grid point:

end end u_M
end end u_R

The larger population is referred to as the resident and a population with average value less than 0.01 is referred to as having been eliminated. The colour coding used in the above algorithm will apply to all the PIP graphs in this study and is summarized as follows:

Colour	Interpretation
Black	X remains the resident and eliminates x .
Blue	x grows and eliminates X .
Red	X remains the resident population but x shows limited grow and co exists with X .
Green	x grows and becomes the new resident but does not eliminate X , they co exist.
Black*	Strategies that generate equivalent populations that co exists.

5.2 Algorithm Outcomes

Table 5.1 tabulates the outcomes of the algorithm for the one, two and three age group cases for r in the range [1 1.7). This range proves to have the higher incidence of irregular periods becoming more regular between 1.6 and 1.7. The second table, Table 5.2, covers the r range [1.7 2] and shows normal periodic behavior but the incidence of quasi periodicity becomes more visible as r approaches 2. When the algorithm delivers a CSS only, it is indicated by the symbol * and if it is an NIS as well, by **. A ‘Garden of Eden’ strategy as discussed in Chapter 2 will be indicated by the symbol G . The actual period will be shown as P_{period} where P_c indicates infinite periods and P_q indicates quasi periodic cases with periods longer than 70.

The ESS strategies with their associated population periods are shown in Figure 5.1.

5.3 Visual Representations

Figures 5.2, 5.4 and 5.5 show examples of some of the findings listed in Tables 5.1 and 5.2 for the different age group situations. For different choices of r in Figures 5.2 and 5.4, the first row shows the growth rate \mathcal{R} , the second row shows the population generated $X(n)$ and the third row the PIP plot. For the three age class case in Figure 5.5, the population row is omitted but will be covered by a later discussion and population Figure 5.7. Figure 5.6 shows both a ‘Garden of Eden’ and ESS outcome

ALGORITHM OUTCOMES FOR r IN THE RANGE $[1, 1.7)$

r	u_0 1 age class	u_0 2 age classes	u_0 3 age classes
1.04	none	none	47.515 $**P_7$
1.19-1.25	none	none	range of $**P_4$
1.26	none	25.498 $**P_5$	16.687 $**P_4$
1.26-1.29	none	$**P_5$	$**P_4$
1.38	11.7050 $*P_3$	none	none
1.42	none	18.92 $**P_c$	none
1.45	none	17.2794 $*$	none
1.46	none	12.86 $**P_3$	none
1.47	none	12.557 $**P_3$	11.04 $*P_2$ & 12 G
1.48	9.8525 $**P_c$	12.275 $**P_3$	10.7960 $**P_2$
1.5	9.5879 $*$	11.768 $**P_3$	10.349 $**P_2$
1.52	none	11.324 $**P_3$	9.946 $**P_2$
1.54	9.0882	10.93 $**P_3$	9.582 $**P_2$
1.55	8.9595 $*$	10.7520 $**P_3$	9.413 $**P_2$
1.56	none	10.582 $**P_3$	9.251 $**P_2$
1.58	8.55 $**P_c$	10.27 $**P_3$	8.947 $**P_2$
1.6	8.000 $*$	9.988 $**P_3$	8.667 $**P_2$
1.62	7.938 $**P_c$	9.735 $**P_3$	8.408 $**P_2$
1.64	7.01 $**P_8$	9.506 $**P_3$	8.166 $**P_2$
1.65	6.495 $**P_2$	9.4 $**P_3$	8.05 $**P_2$
1.66	6.364 $**P_2$	9.298 $**P_3$	7.939 $**P_2$
1.68	6.123 $**P_2$	9.1109 $**P_3$	7.726 $**P_2$

Table 5.1: CSS and ESS outcomes for the r range $[1, 1.7)$. This range proves to have the higher incidence of irregular periods becoming more regular between 1.6 and 1.7.

for the same r . Figure 5.3 illustrates how by managing the iteration amounts, chaotic effects can be smoothed considerably.

5.3.1 Discussions from the gallery

For some of the interesting finds in Tables 5.1 and 5.2, the growth rate, PIP and population plots were generated and are shown in Figures 5.1 till 5.8. All three age group cases are included in this visual investigation and at the end of this section, one will have a better understanding of the differences between the CSS, ESS, ESTs and ‘Garden of Eden’:

1. CSS, NIS and ESS: From the bottom rows of Figures 5.2, 5.4 and 5.5, the strategies testing ESS are characterized by a vertical line through $u_R = u^*$ passing from black red to red black and a horizontal line passing from blue

ALGORITHM OUTCOMES FOR r IN THE RANGE [1.7, 2]

r	u_0 1 age class	u_0 2 age classes	u_0 3 age classes
1.7	5.904 $**P_2$	8.942 $**P_3$	7.524 $**P_2$
1.72	5.704 $**P_2$	8.793 $**P_3$	7.332 $**P_2$
1.74	5.521 $**P_2$	8.6684 $**P_3$	7.149 $**P_2$
1.76	5.3518 $**P_2$	8.5637 *	6.9738 $**P_2$
1.77	5.272 $**P_2$	8.49 $**P_q$	6.888 $**P_2$
1.78	5.195 $**P_2$	8.4039 *	6.8038 $**P_2$
1.8	5.0499 $**P_2$	8.204 *	6.6384 $**P_2$
1.82	4.914 $**P_2$	7.984 *	6.4763 $**P_2$
1.83	4.85 $**P_2$	7.87 *	none
1.84	4.7878 $**P_2$	7.754 *	none
1.86	4.6689 $**P_2$	7.521 *	none
1.88	4.557 $**P_2$	7.291 *	none
1.9	4.4517 $**P_2$	7.065 *	none
1.91-1.98	range of $**P_2$	none	none
1.99	4.0404 $**P_2$	6.16 $**P_q$	none

Table 5.2: CSS and ESS outcomes for the r range [1.7, 2] and shows more periodic behavior but the incidence of quasi periodicity becomes more visible as r approaches 2.

green red to red green blue through (u_*, u_*) . Other vertical and horizontal lines through strategies in u^* 's close neighborhood will not have this property. The vertical line through u^* from black to black shows the non invasibility of the established X^* and is what makes u^* a CSS and the horizontal line from blue to blue shows the non invasibility of X^* even at very small population densities x and is what makes u^* a NIS and the combination of these two properties is what makes u^* an ESS. The red area in the immediate neighborhood shows that the two competing strategies are so close in value that they practically generate the same population. This is also evident from the black/blue growth function plots where there is a neighborhood of contact between the black \mathcal{R} graph and the blue \mathcal{M} graph. The longer the contact/overlap, the wider the red area is as shown in Figure 5.5 (a). The green areas in the PIP plots represent strategy combinations close enough to the ESS where x is growing but at a much smaller pace while the resident loses ground but not to the extent of extinction.

2. 'Garden of Eden': Figures 5.5(a), 5.6(a) and (b) show the situation where for $r = 1.47$ the strategy $u_R = 12$ is a 'Garden of Eden' ESiS but $u_R = 11.04$ is a CSS provided the search is started close enough to 11.04. This implies that the succession of strategies will converge to 11.04 if evolution started on the left of this value, but if evolution started from the right, there will not be a converging

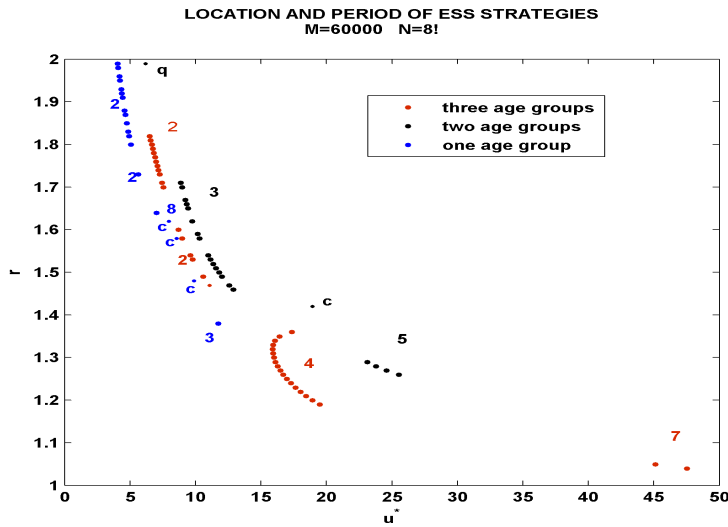


Figure 5.1: ESS strategies, that is, strategies testing both CSS and NIS, for the experimental one, two and three age group cases.

series of CSS strategies as there is not one but many strategies characterized by a vertical line passing from black to black, with the line through 12 showing a lessor red sharing area. Horizontal lines through these two strategies do not pass from blue to blue, and they are therefore not NIS strategies. A CSS with a protected dimorphism² are those depicted by black areas above and below the

²Limited stable co existence.

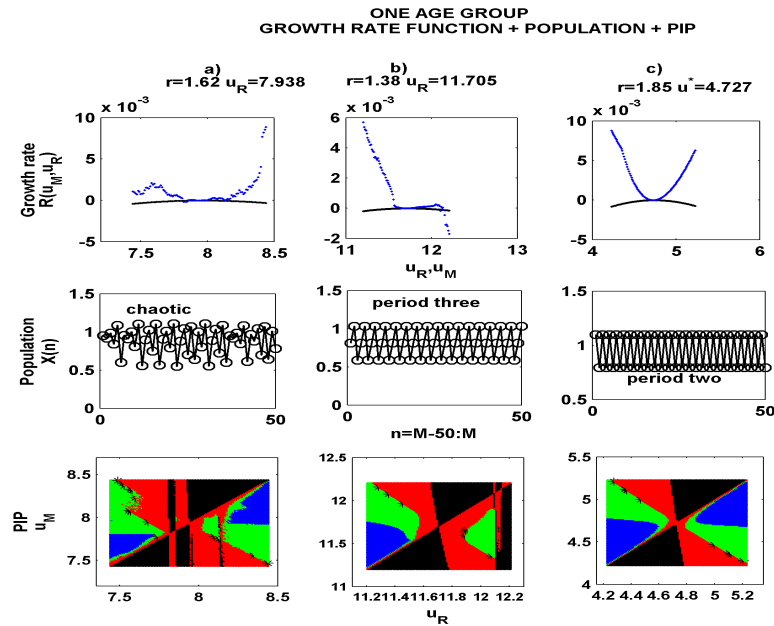


Figure 5.2: The combination of the growth rate \mathcal{R} , the generated recruitment population $X(n)$ and the PIP's for the one age group experimental situation is shown in column (a) for $r = 1.62$, column (b) for $r = 1.38$ and in column (c) for $r = 1.85$.

vertical line through $u_R = u^*$, overlapping this vertical somewhat but this must not be true for vertical lines through other neighborhood strategies which was the case for $u_R = 12$. Small perturbations in u^* should evolve back to u^* , this makes an ESS more special than other strategies.

3. What does chaos look like?: Figure 5.2(a) shows what a chaos inducing strategy

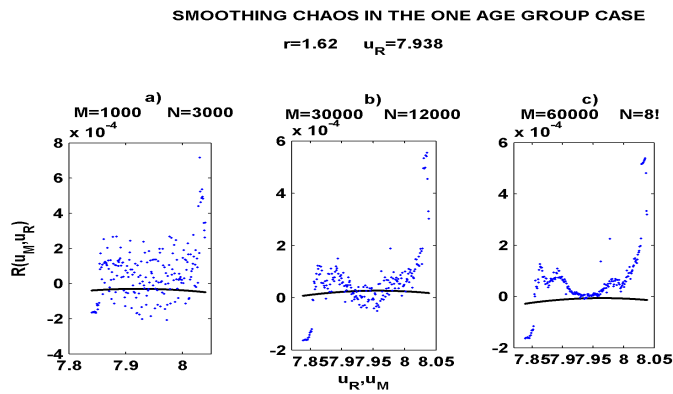


Figure 5.3: The chaotic situation brought on by the choice $r = 1.62$ in the one age group case. Figures (a), (b) and (c) show progressively smoother NIS graphs when the initial amount of iterations M and the periodic amount N is increased.

looks like on a growth rate, population and PIP plot. This strategy tests CSS with a vertical line passing from black to black through $u_R = 7.938$ on the PIP graph and the black maximum plot on the growth rate graph. The irregular pattern on the population graph, the blue scattered almost minimum plot on the growth rate graph and the horizontal line not passing from blue to blue

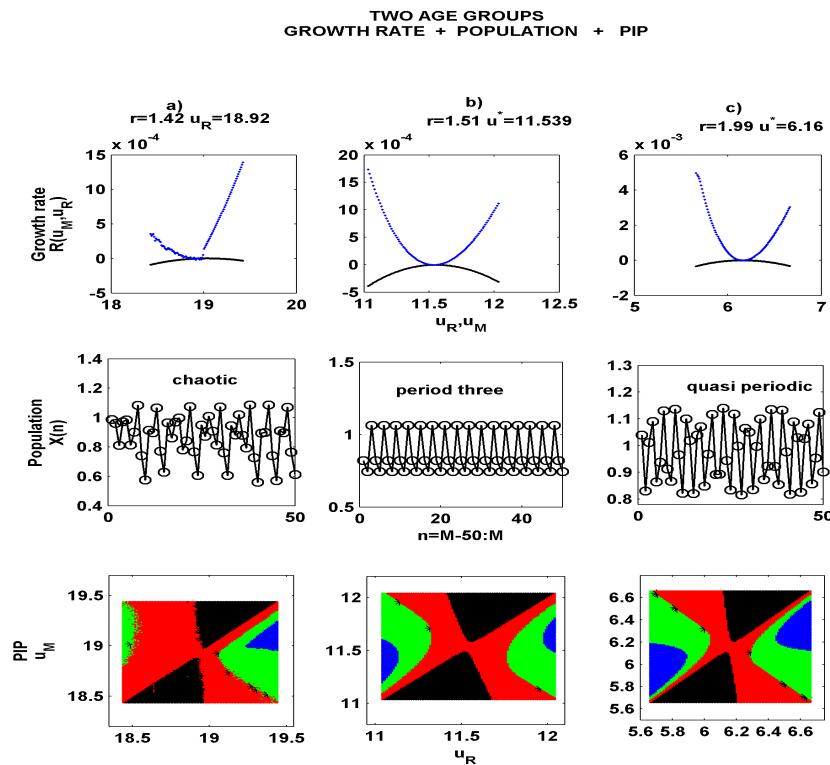


Figure 5.4: The combination of the growth rate \mathcal{R} , the generated recruitment population $X(n)$ and the PIP's for the two age group experimental situation is shown in column (a) for $r = 1.42$, column (b) for $r = 1.51$ and in column (c) for $r = 1.99$.

but rather from a region of slow growth to co existence to loosing to sharing and so on is what labels this strategy as one that induces chaotic behavior. Figures 5.3(a), (b) and (c) show how the iteration amounts M and N affect the smoothness of the blue plot on the growth rate graph. A combination of very large M and N values might very well converge to a smooth curve..eventually!

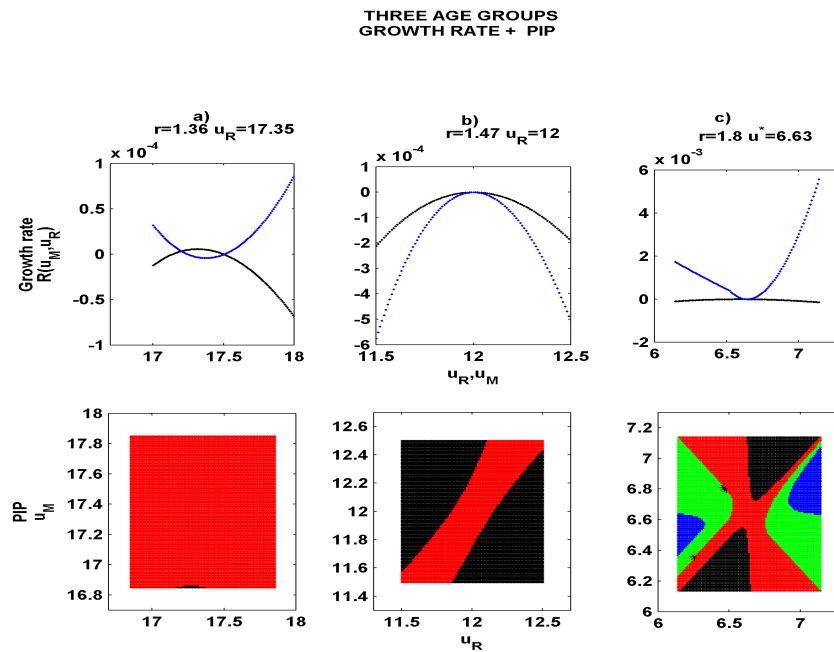


Figure 5.5: The combination of the growth rate \mathcal{R} and the PIP's for the three age group experimental situation is shown in column (a) for $r = 1.36$, column (b) for $r = 1.47$ and in column (c) for $r = 1.8$.

4. Quasi periodicity: A typical example of a quasi periodic ESS is in the two age class structure for $r = 1.99$ as shown in Figure 5.4(c). The population graph has a sinusoidal outline. The two age group case leans itself towards chaotic, normal periodic and quasi periodic examples as is shown in Figure 5.4(a), (b) and (c) respectively. Chaotic solutions are associated with smaller r values

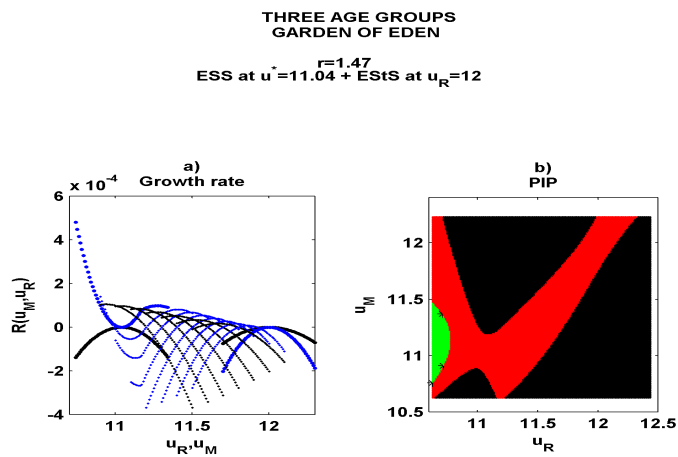


Figure 5.6: Figure (a) shows the progression of the growth function \mathcal{R} from $u = 11$ until $u = 12$ for the three age group case. The strategy $u_R = 11.04$ will only be a CSS strategy in a very small neighborhood of this value, with evolutionary convergence from the left but only partially so from the right. The horizontal line through this value does not pass from blue to blue. If evolution starts at $u = 12$, natural selection will be indifferent as to the direction of evolution for future strategy improvement as shown by (b), where vertical lines through any neighborhood strategy of $u = 12$ will have the same property as $u = 12$ and can lead to evolutionary branching.

(the battle to survive is usually not pretty) and quasi periodicity with larger r

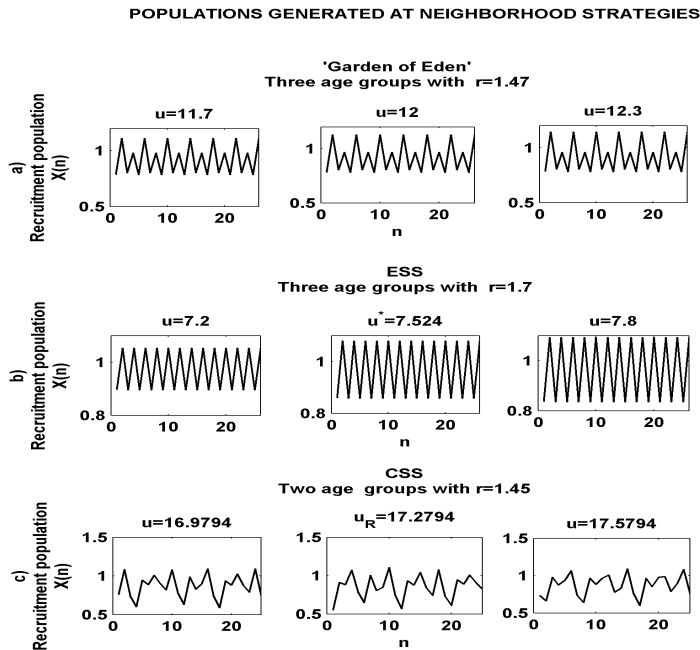


Figure 5.7: Figure (a) shows that for strategies smaller and bigger than the 'Garden of Eden' strategy $u = 12$, the populations generated are almost the same. There is nothing special about $u = 12$ it does not represent a better fit about \mathcal{K} in comparison to its neighbors. Figure (b) shows what an ESS situation should represent concerning neighboring strategies. The value $u^* = 7.524$ represents the better fit with $u = 7.2$ being too small and $u = 7.8$ too extreme. Figure (c) shows the populations generated for variations on the CSS strategy $u = 17.2794$. Similar conclusions can be made as in Figure (a).

values.

5. Comparing populations: From Figure 5.7(a) the ‘Garden of Eden’ strategy does not generate a population with more \mathcal{K} advantage than those in its neighborhood. For choices slightly larger and smaller, similar if not exact populations are generated. Figure 5.7(b) shows how an ESS strategy is different in this regard, offering a happy midway between choices larger or smaller. When the smaller population (on average less than one) is exposed to u^* which is larger than its own strategy, the ratio:

$$\left(\frac{X_R}{\mathcal{K}}\right)^{u^*} < \left(\frac{X_R}{\mathcal{K}}\right)^{u_R} \quad (5.7)$$

and the density mechanism

$$\psi(u^*, X_R) = \frac{r}{1 + \left(\frac{X_R(n)}{\mathcal{K}}\right)^{u^*}} \quad (5.8)$$

will be larger (an increase in \mathcal{R}) than the equilibrium state it was in which is necessary for the new combination to evolve to a new balance. Similarly, when the larger population generated at a larger strategy value is exposed to the smaller u^* , the ratio (5.7) of the population (with values exceeding one) raised to the smaller u^* will initiate a larger $\psi(u^*, X_R)$ which will again increase \mathcal{R} . An ESS strategy should offer a better fit around \mathcal{K} with respect to those close by. The same situation is seen for the CSS strategy in 5.7 c).

6. It was seen that a CSS strategy is not necessarily a NIS as well. There is certainly a difference in the invasibility properties of an established population and one that has just started out. A case where there exists a NIS but not a CSS was not found during the investigation, which does make sense.

5.4 The Pacific Sardine Population

A stochastic age-structured model with a Shepherd driven recruitment function was used to study the Pacific sardine (*Sardinops caeruleus*) population of the Gulf of California in [91]. The study was done over the period 1972 - 1990 and incorporated fishing mortality³. The age-structured data was estimated by Cisneros-Mata *et al* where the nonlinear Marquardt (FISHPARM) algorithm was used to fit the Shepherd recruitment function to this data [91]. The stock-recruitment function used was:

$$\psi(n) = \frac{aP(n-1)}{1 + \left(\frac{P(n-1)}{b}\right)^c} \quad (5.9)$$

³Death caused by fishing.

LIFE TABLE FOR THE PACIFIC SARDINE [1979 - 1989]

yr	$\psi(u, X) \cdot X$	x_1	x_2	x_3	x_4	x_5	x_6
1979	5874631	4090689	1264492	290707	21628	1476	1
1980	8562187	2682036	1528759	348017	37453	8882	600
1981	9955486	3949767	987030	428444	18877	3190	2047
1982	14500033	615188	1377710	130533	17897	2904	463
1983	22115802	6626972	1851061	537762	4379	607	108
1984	28562340	10078614	2081420	367509	13873	362	21
1985	23633075	13203679	4145572	686667	46353	5218	43
1986	11851629	10637752	5270339	1564716	138469	16989	2104
1987	9961348	5432792	4184076	1572530	260840	34653	2459
1988	5810251	4682059	2297139	1250580	290648	64595	7548
1989	3316850	2222967	1547267	450867	163179	51179	11950

Table 5.3: Life table for the Pacific sardine *Sardinops Caeruleus* population of the Gulf of California, Mexico. X refers to the recruits and the combination $\psi(u, X)X$ to the successful recruits after exposure to the density function. All values $\times 10^3$.

Where P is the spawning stock biomass⁴, a is the maximum expected spawning rate per spawning adult, b is the fish capacity the environment can maintain and c is the measure of density control exercised by the spawning stock. The data fit showed that a, b and c were respectively 2.697, 1.417×10^{10} and 6.499 [91]. Since the density function in this study is formulated around the recruits X and not the entire spawning stock P , the interpretation of the parameters a and b will be different in this study. The data provided per age group from 1972 until 1990 is tabulated in Table 5.3 (all values $\times 10^3$).

Calculating the average survival rates from equation (3.3) with

$$s_i = \frac{x_{i+1}(n+1)}{x_i(n)}, \quad (5.10)$$

gives

$$s_0 = 0.42, \quad s_1 = 0.38, \quad s_2 = 0.29 \quad (5.11)$$

$$s_3 = 0.11, \quad s_4 = 0.22, \quad s_5 = 0.17 \quad (5.12)$$

The average birth rate, assuming that $b_i = b$ for $i = 1, \dots, 6$, cannot be calculated from the above table as the small fish caught in the study is not the total recruitment population but just those that successfully hatched from the egg stage after

⁴The total weight of the fish old enough to spawn.

density control had (already) taken place. The parameter a in (5.9) represents the number of recruits per adult and has value 2.697. The growth rate r represents the maximum proportion of eggs that successfully hatch and live to form the recruitment population which is approximately $a = 2.697$ per spawning adult. Kishida and Wada [66] did a similar study on the Japanese sardines *Sardinops melanosicus* for which they estimated r to be between 0.2 and 1.4. It will therefore not be out of line to choose r in this study to be 1.25, implying from (1.36) and (1.38) that an initially small recruitment population can replace itself as well as add a quarter of its current density to the survival tally. The average birth rate b was experimentally determined by running the algorithm over a range of b values in the interval $[1.5, 4]$ for $r = 1.25$ and the best results, with the algorithm delivering an ESS, were found for $b = 2.3$. It was found in general that the smaller r is, the larger b must be to generate ESS solutions. This makes sense as a high birth rate would require serious density curbing which implies r values less than one which initiates immediate damping.

Observations made by Cisneros-Mata *et al* in [29] were that the recruitment population showed a growth spurge every five to ten years and the sardine population as a whole showed periodic tendencies of approximately 60 years. A periodic environmental conditions can be simulated with a sin graph and Cisneros-Mata *et al* used a sin function to model the survival rates of the sardines as follows:

$$s(t) = s_0 + d \sin\left(\frac{2\pi t}{T}\right) \quad (5.13)$$

Here $s(t)$ is the survival rate at time t , s_0 is the original survival rate, d is the amplitude and $T = 60$ the period. In this study, equation (5.13) will instead be used to simulate a fluctuation in r as suggested by Kishida and Wada [66] for the Japanese sardine.

Incorporating a fluctuating r into the algorithm, is a simple task of substituting the current reference to r in Routines 2 and 3 with the expression:

$$r(ii) = r0 + d * \sin((2 * pi * ii)/T) \quad (5.14)$$

Calculating suitable values for $r0$, d and T , the data in Table 5.3 must first be suitably scaled:

If \mathcal{K} is taken as one, the data in Table 5.3 must be scaled accordingly. The scaling factors were chosen as a result of the following observations (values $\times 10^3$):

1. In order to compare the algorithm generated $\psi(u, X)X(n)$ to the real values in the second column of Table 5.3, the data in this column first had to be divided by 25×10^6 . The reason for this was that the population was still allowed to grow in 1983 but when it reached its peak value in 1984, the density mechanism kicked in and brought their total down again in 1985. It can therefore be concluded that

\mathcal{K} was exceeded by the total in 1984 but not that of 1983, which means that \mathcal{K} must lie somewhere between these two values, which is approximately 25×10^6 . The recruitment population plot in Figure 5.8(a) shows the comparison.

2. The total population values were calculated by summing the rows of Table 5.3. The peak value and the values before and after were calculated to be 35385283, 45699744 and 37812920. This implies that \mathcal{K} must lie somewhere between 35385283 and 45699744 and was chosen to be 40×10^6 . The population totals were divided by 40×10^6 and compared to the population totals as calculated by the algorithm in Figure 5.9(b).

A good choice for r_0 is $r_0 = 1.25$ as this value will allow for fluctuations in the range $[0.2, 1.4]$ as proposed by Kishida and Wada. The proposed T values were $T = 5$ and $T = 10$ and the amplitude d of the fluctuation is usually a value between 0.4 and 0.9. From the scaled real $\psi(u, X)X$ data (red graph) shown in Figure 5.8, the periodic tendency is approximately $T = 10$ and the amplitude will be slightly larger for X (as opposed to that of $\psi(u, X)X$), approximately $d = 0.9$. For the scaled real total population data (red graph) in Figure 5.9 the periodic tendency is approximately $T = 10$ and the amplitude approximately $d = 0.9$.

The algorithm determined the best fit combination under constant \mathcal{K} conditions and the results are shown in Figures 5.8(a) and (b). As predicted, the period $T = 10$ and amplitude $d = 0.9$ proved to be the best fit for the current state of the sardine population as shown in the recruit density graph of Figure 5.8(a). The ESS strategy $u^* = 2.4985$ is very small and r oscillates between 2.15 and 0.35 which is both very large and very small. As explained in Chapter 1, r will be large when there is an abundance in resources, but this comes with the risk of over populating the environment, the females will then encourage competition amongst the recruits by under dispersing them (associated with small u values) on resources [52]. The upper bound of r overrules the lower bound. Figure 5.8(b) shows the results for the period choice $T = 5$, which predicts a tighter fit around \mathcal{K} and larger u values. ESS strategies could not be found for $T = 5$ and $d > 0.6$ which is why this choice cannot offer a good simulation for the real data. The tendency seems to be that the larger the oscillation amplitude, the larger T will be in this case. Figure 5.8(b) also shows the outcomes for a constant $r = 1.25$, predicting a period two oscillation which is probably the strategy the population will continuously strive towards amidst varying conditions. Note that \mathcal{K} for $X(n)$ is taken as one, which is why the oscillations of the density reduced $\psi(n, X(n))X(n)$ will be around a value slightly less than one. Figures 5.9(a), (b) and (c) show the eventual (total) populations generated by the algorithm for different periods and amplitudes. Figure 5.9(b) shows the best fit for the real (total population) sardine data. Figure 5.9(c) shows the outcome if $T = 60$.

The only amplitude that generates an ESS in this case is $d = 0.2$. There are CSS strategies at $u_R = 11.011$ for $d = 0.4$ and $u_R = 3.455$ for $d = 0.6$.

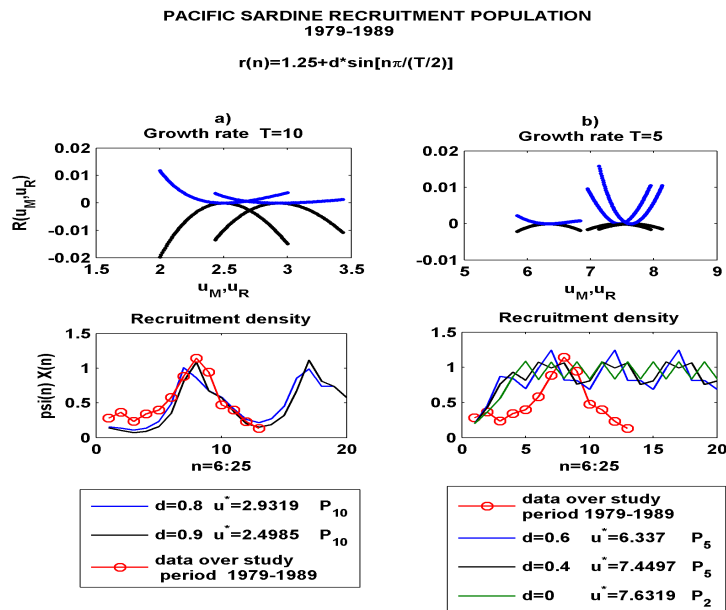


Figure 5.8: Column (a) shows the CSS/NIS combinations for the different amplitudes of the sin function when $T = 10$. For the choices $d = 0.8$ and $d = 0.9$ the algorithm produced ESS strategies 2.9319 and 2.4985 respectively. Density simulations of the successful recruits are compared to the actual data showing a close match with the choice $d = 0.9$. Column (b) shows the outcomes for the period choice $T = 5$ which predicts eventual tighter oscillations around \mathcal{K} .

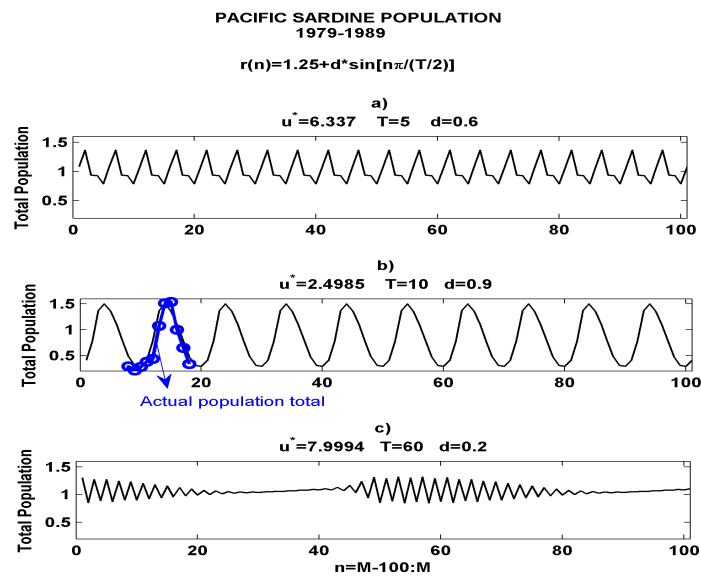


Figure 5.9: Figures (a), (b) and (c) respectively show the ESS strategies 6.337, 2.4985 and 7.9994 for amplitudes 0.6, 0.9 and 0.2 and periods 5, 10 and 60. Figure (b) shows that the period 10 situation with $d = 0.9$ offers the better fit for the current total sardine population densities.

Chapter 6

The Stage-Structured Model

Complicating simple population dynamics by introducing age-structure is well worth the trouble provided age specific data is available from life tables. Models designed to accommodate age-structure reveals tendencies within populations over time, which can be used to save certain populations from extinction or over population. What does one do, however, when the population involved is of such a nature that it is difficult or even impossible to acquire age specific data? What if the only data available is that which is practically observable, such as size or phase? For such populations, age-structure is unpractical and stage-structure, which is ages sorted into common weight, phase or size stages, will be used instead [21]. This chapter will discuss the formulation of a stage structured population as well as show the relationship between the coefficients of the age and stage structured models.

6.1 Defining Stage-Structure

For fish, insects and other challenging population types, age structured life tables are formulated from an averaging process of the stages that can be identified [50]. Designing a model specifically for stage-structure and adding a density control mechanism for the recruitment stage will be explained next.

6.1.1 Setting the stage

To formulate a stage-structure with m stages, an i stage S_i is identified with survival rate f_i and birth rate B_i as opposed to an i age x_i with associated survival and birth rates s_i and b_i . For the construction of a model describing the population's progress through a stage classification, the following assumptions will be made:

1. The growth stages cover sufficiently large intervals in the growth pattern so that each individual will enter successive stages and not skip a stage.
2. Not all the individuals in stage S_i will survive from time n until time $n + 1$. The proportion of the population in stage i that survive from time n till $n + 1$ whether they move up one stage or not will be shown as $f_i S_i(n)$ where f_i is similar to the survival rates s_i used in the age structured model.
3. The proportion of these survivors that graduate to the next stage from time n to $n + 1$ will be shown as $p_i f_i S_i(n)$ where p_i is in the range $[0, 1]$, and the proportion that stays behind will be shown as $q_i f_i S_i(n)$ where $q_i = 1 - p_i$.
4. The population in stage $i + 1$ at time $n + 1$ is the sum of the proportion in stage i that qualifies to enter stage $i + 1$ and the proportion already in stage $i + 1$ that stayed behind. That is, for $i = 1, \dots, m - 1$:

$$S_{i+1}(n + 1) = q_{i+1} f_{i+1} S_{i+1}(n) + p_i f_i S_i(n) \quad (6.1)$$

$$= Q_{i+1} S_{i+1}(n) + P_i S_i(n) \quad (6.2)$$

$$\text{where } Q_i = q_i f_i \text{ and } P_i = p_i f_i \quad (6.3)$$

5. If B_i is the birth rate of the females in stage (not age) i then, similar to the age structured model, the number of recruits $Y(n)$ at time n from all the stages are:

$$Y(n) = B_1 S_1(n) + B_2 S_2(n) + \dots + B_m S_m(n) \quad (6.4)$$

6. A Shepherd density mechanism is incorporated into the recruitment stage and defined as stage 0 [50]:

$$S_o(n) = \psi(n) Y(n) \quad (6.5)$$

and represents the recruits that have successfully 'graduated' from the density program, which is a once off stage. If the proportion f_o of these recruits make it to stage 1 then:

$$S_1(n + 1) = Q_1 S_1(n) + P_o \psi(n) Y(n) \quad (6.6)$$

Where it is assumed that all the recruits graduate to the first stage from time n to $n + 1$ and that no one stays behind in stage zero, therefore, $p_o = 1$ and

$P_0 = f_0$. Stage-structure usually comprises of the following four stages [95]:

$$\text{Recruits } Y(n) = \sum_{i=1}^4 B_i S_i(n) \quad (6.7)$$

$$\text{Young adults } S_1(n+1) = Q_1 S_1(n) + P_0 \psi(n) Y(n) \quad (6.8)$$

$$\text{Prime adults } S_2(n+1) = Q_2 S_2(n) + P_1 S_1(n) \quad (6.9)$$

$$\text{Old adults } S_3(n+1) = Q_3 S_3(n) + P_2 S_2(n) \quad (6.10)$$

6.1.2 Determining the values of P and Q

Calculating the relationship between the age and stage-structure parameters, the progress of a hypothetical group of recruits $Y(n)$ entering the system at time n will be followed over their life span of say 7 years. We start with an age structured model with the parameters associated with age-structure, then using the definition for L_n from Chapter 3 and introducing the notation:

$$Z(n) = \psi(u, Y(n)) Y(n), \quad (6.11)$$

$$\text{and stage } i = S_i, \quad (6.12)$$

the age structured version of the progress of the experimental group $Y(n)$ over 7 time intervals will look as follows:

$$\begin{aligned} X^o(n) &= Z(n) \\ X^o(n+1) &= s_o Z(n) = L_0 Z(n) \\ X^o(n+2) &= s_1 X^o(n+1) = L_1 Z(n) \\ X^o(n+3) &= s_2 X^o(n+2) = L_2 Z(n) \\ X^o(n+4) &= s_3 X^o(n+3) = L_3 Z(n) \\ X^o(n+5) &= s_4 X^o(n+4) = L_4 Z(n) \\ X^o(n+6) &= s_5 X^o(n+5) = L_5 Z(n) \\ X^o(n+7) &= s_6 X^o(n+6) = L_6 Z(n) \end{aligned} \quad (6.13)$$

Recall that $Z(n)$ represents the eggs that have successfully hatched into recruits. Only the proportion f_0 of these recruits will survive to stage S_1 at time $n+1$ on account of their compromised survival skills. S_1 is usually also a once off stage, not sharing common parameters with any of the others stages and will last only one time interval, that is, this *new* batch entering stage 1 will not share this stage with recruits from a previous *old* batch and is given by:

$$S_1 = (0)_{old} + (X^o(n+1))_{new} \quad (6.14)$$

$$= (0)_{old} + (L_0 Z(n))_{new} \quad (6.15)$$

Where $s_o = f_o$. If $X^o(n+2)$ and $X^o(n+3)$ share similar properties such as a common survival rate ($s_2 = s_3 = f_2$) and birth rate ($b_2 = b_3 = B_2$), they can be grouped together as S_2 :

$$S_2 = (X^o(n+3))_{old} + (X^o(n+2))_{new} \quad (6.16)$$

$$= (L_2Z(n))_{old} + (L_1Z(n))_{new}, \quad (6.17)$$

where $X^o(n+2)$ represents the *new* addition to S_2 and $X^o(n+3)$ represents those that stayed behind (*old*) in this stage. Similarly, stage 3 and stage 4 can be defined, on account of similar properties, as:

$$S_3 = (X^o(n+5) + X^o(n+6))_{old} + (X^o(n+4))_{new} \quad (6.18)$$

$$= (L_4Z(n) + L_5Z(n))_{old} + (L_3Z(n))_{new} \quad (6.19)$$

$$S_4 = (0)_{old} + (X^o(n+7))_{new} \quad (6.20)$$

$$= (0)_{old} + (L_6Z(n))_{new} \quad (6.21)$$

Coming back to the stage model (6.2), the above separation into *old* and *new* can be compared for stage i to Q and P :

$$(\cdot)_{old} = Q_i S_i \quad (6.22)$$

$$(\cdot)_{new} = P_{i-1} S_{i-1} \quad (6.23)$$

Comparing the *new* entries for each stage using (6.23) shows that:

$$S_1 : L_0Z(n) = P_0 S_0 \quad (6.24)$$

$$= P_0 Z(n) \text{ from (6.5)} \quad (6.25)$$

$$P_0 = L_0 \quad (6.26)$$

$$= f_0 \quad (6.27)$$

$$S_2 : L_1Z(n) = P_1 S_1 \quad (6.28)$$

$$= P_1 L_0 Z(n) \text{ from (6.15)} \quad (6.29)$$

$$P_1 = \frac{L_1}{L_0} \quad (6.30)$$

$$= f_1 \quad (6.31)$$

$$S_3 : L_3Z(n) = P_2 S_2 \quad (6.32)$$

$$= P_2 (L_2Z(n) + L_1Z(n)) \text{ from (6.17)} \quad (6.33)$$

$$P_2 = \frac{L_3}{L_1 + L_2} \quad (6.34)$$

$$= \frac{f_2^2}{1 + f_2} \quad (6.35)$$

$$S_4 : L_6 Z(n) = P_3 S_3 \quad (6.36)$$

$$= P_3 (L_4 Z(n) + L_5 Z(n) + L_3 Z(n)) \quad \text{from (6.19)} \quad (6.37)$$

$$P_3 = \frac{L_6}{L_3 + L_4 + L_5} \quad (6.38)$$

$$= \frac{f_3^3}{1 + f_3 + f_3^2} \quad (6.39)$$

In general, for S_i of length w :

$$P_i = \frac{f_i^w}{\sum_{k=0}^{w-1} f_i^k} \quad (6.40)$$

$$Q_i = f_i - P_i \quad (6.41)$$

Compiling an all inclusive difference equation, as was done for the age structured case in Chapter 3, is not a practically implementable process. In this case it is more convenient to keep the stage-structure as shown in equations (6.8) to (6.10) followed by the calculation of the next generation population Y using (6.7) after each time interval. For a stage-structure spanning m time intervals, the calculation for \mathcal{R} will again be the ratio:

$$\mathcal{R}(u, \bar{Y}(u)) = \frac{Y(n)}{Y(n-m)} \quad (6.42)$$

$$\text{where } \bar{Y}(u) = [Y(n-1), \dots, Y(n-m)] \text{ all calculated at } u \quad (6.43)$$

6.2 The Kudu Population

A stage structured population model was developed by Norman Owen Smith for the kudu population (*Tragelaphus strepsiceros*) in South Africa's Kruger National Park. The data followed a ten year study, documenting the relationships between the annual survival rates of a particular age group, resource availability and rainfall during this time. The birth and survival rates are actually dynamic variables based on rainfall as rain controls resource abundance which in turn controls births and deaths. For this study, however, these values will be calculated using the average rainfall over the 10 year study period. The kudu in the study area were identified by their stripe variation which made female stage specific data collection practically possible. If R is the annual rainfall (mm) and H is the population biomass density (kg/km^2) then the ratio $\frac{R}{H}$ represents the resource to consumer density ratio. Clearly, if the density ratio is low, mortality will be high and vice versa. Mortality should therefore be an inverse function of this ratio. Getz (1993) [51] suggested the hyperbolic mortality

equation for stage i as being

$$M_i = a_i + \frac{c_i}{\frac{R}{H}} \quad (6.44)$$

The values of a_i and c_i were calculated from fitting the actual data to this equation. The survival rates f_i are then calculated as

$$f_i = 1 - M_i \quad (6.45)$$

The stage specific survival rates were calculated using (6.45) at mean resource to consumer density ratio $\frac{R}{H} = 1.5$ and a_i and c_i values suggested by Norman Owen Smith with the birth rate of each stage given as $B_i = 0.95$ for $i = 3, 4$ and $B_i = 0$ for $i = 1, 2$ [95, 51]. The values are tabulated in Table 6.1.

STAGE SPECIFIC DATA FOR THE KUDU POPULATION [1974-1984]

i	S_i	duration (yr)	a_i & c_i	f_i	B_i
0	recruits	1	0.014 & 0.760	0.479	0
1	yearling	1	0.005 & 0.197	0.864	0
2	pre-prime females	1	0.027 & 0.082	0.918	0
3	prime female	4	0.027 & 0.082	0.918	0.95
4	old female	8	-0.069 & 0.357	0.831	0.95

Table 6.1: Stage specific survival rates calculated with density ratio $\frac{R}{H} = 1.5$ for the kudu population in the Kruger National Park .

The values of P_i, p_i, Q_i and q_i are calculated, using (6.52) and (6.3), to be:

$$\bar{P} = [0.8640 \ 0.9180 \ 0.2009 \ 0.0497] \quad (6.46)$$

$$\bar{p} = [1 \ 1 \ 0.2189 \ 0.0599] \quad (6.47)$$

$$\bar{Q} = [0 \ 0 \ 0.7171 \ 0.7813] \quad (6.48)$$

$$\bar{q} = [0 \ 0 \ 0.7811 \ 0.9401] \quad (6.49)$$

The carrying capacity \mathcal{K} will refer to the average number of females / km^2 and is approximately 1.23 females/ km^2 . The parameter r is the maximum growth rate of the recruits at low recruit densities. Since the growth rate of the kudu population in the Kruger National Park stabilizes on approximately 0.32, and the Shepherd model stabilizes on approximately $\frac{r}{2}$, the value of r is estimated to be $r \approx 0.64$ [95]. The parameter f_0 is then the proportion of these recruits that survive to the next age class. The algorithm calculates the quasi periodic CSS to be $u_R = 19.98$ if $r = 0.64$. When comparing the total population generated at u_R (black) with the actual data (red) in

Figure 6.1(b), it is clear that the assumptions made are not compatible with the true situation. This can be ascribed to many factors, amongst others, the importance of rainfall variation in the model. Inspired by the results in Chapter 5 where a sinusoidal growth rate was used for the Pacific sardine population, the changing environment will be simulated again by letting:

$$r(n) = r_o + d \sin\left(\frac{2n\pi}{T}\right) \quad (6.50)$$

Where r_o is the base intrinsic growth rate value and taken to be 0.64. Norman Owen Smith's study also shows a 20 year tendency between population peaks [95]. For this reason $T = 20$ years. It was found that the amplitude $d = 0.6$ (blue) gave the best results as shown in Figure 6.1(b). The algorithm found the ESS to be at $u^* = 6.187$ which is very different to the CSS for the constant $r = 0.64$. This is as a result of the boosting property of the sinusoidal graph where the females must now be a little bit more careful not to over populate the area.

6.3 On The Stage

In a stage structured population model where f_i is the stage survival rate from time n to $n + 1$ (whether they move up one stage or not) and p_i is the proportion of these survivors that graduate to the next stage over this time and q_i is the proportion that stays behind and $q_i = 1 - p_i$, the population model takes on the form:

$$S_i(n + 1) = Q_i S_i(n) + P_{i-1} S_{i-1}(n) \quad (6.51)$$

where $P_i = f_i p_i$ and $Q_i = f_i q_i$ and

$$P_i = \frac{f_i^w}{\sum_{k=0}^{w-1} f_i^k}$$

or rather $p_i = \frac{P_i}{f_i}$ (6.52)

where w is the length (number of time intervals represented by this stage) of stage i .

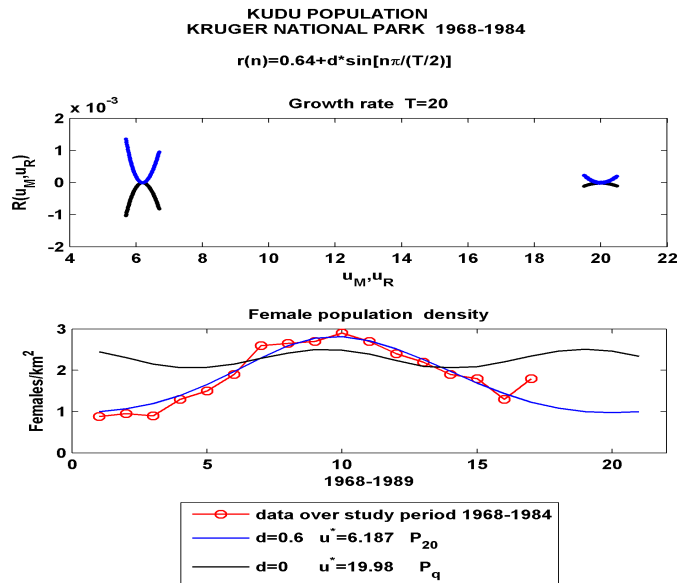


Figure 6.1: (a) The CSS/NIS combinations for the different amplitudes of the sine function when $T = 20$. For the choices $d = 0$ and $d = 0.6$ the algorithm produced a CSS at $u_R = 19.98$ and an ESS at $u^* = 6.187$. (b) Population density simulations of the successful recruits are compared to the actual data showing a close match for the choice $d = 0.6$.

“What about elevenses? Luncheon? Afternoon tea? Dinner? Supper? He knows about them, doesn't he?”

- Lord of the Rings, J.R.R. Tolkien

Chapter 7

In Conclusion

*One strategy to rule them all,
one strategy to find them,
one strategy to bring them all
and in evolution bind them..*

This study was inspired by Schoombie and Getz [105]. Their investigation into the properties of the strategy parameter in the non age structured Shepherd driven population model was extended in this study to the age structured case. This gave rise to quite a few questions, namely:

1. Where should the density mechanism be placed in an age structured model?
2. Will there be ESS's similar to those in the non age structured case?
3. What exactly is an ESS and how does it differ from a CSS or a NIS?
4. What are the graphical invasibility properties of the ESS when competing with other strategies?
5. What deductions concerning the population's future can be made from knowing what the ESS strategy is?

After an extensive literary study covering ESS's, adaptive dynamics, game theory and population simulation models, I realized that the inner workings of natural selection can only be fully understood by deriving the ESS criteria for oneself by applying adaptive dynamics to the strategy driven competition model. This exercise led to a better understanding of natural selection, the role of the fitness function, the fitness gradient and the mathematical differences between the CSS, NIS and ESS.

The first challenge was choosing the age structured model and allocating the shepherd density function in this structure. Fortunately, Getz in [50] not only formulated the age structured model used in this study, but also suggested that the density function be incorporated as the recruitment survival parameter. This is a practical choice since newborn survival decreases as their densities increase. Compiling an expression for the fitness function involved converting the age structured model into a difference equation in terms of the recruitment population. This made it possible to define the recruitment fitness function as the ratio of the recruitment population calculated over one period. Only one more obstacle had to be overcome and that was applying the ESS criteria to this fitness function. The criteria required the calculation of the fitness gradient, several times in fact, which necessitated the construction of a custom made strategy optimization algorithm. This algorithm not only calculated the fitness gradient but determined the direction of evolution, followed it and found the ESS if it existed.

Naturally one would like to know what makes an ESS different to the CSS, NIS and EStS. For this reason, both the geometric invasibility properties and the population advantage of the ESS were visually represented. The first was done for different outcome scenarios of the competition model formulated in [105] and applied to the age structured model, and the second was done by generating populations at other neighborhood strategies. Together, these two plots offered a visual clarification of what makes an ESS stand out above the rest. The above questions can now be answered:

1. The Shepherd function was incorporated at the recruitment level of the age-structure. This is a practical choice as the recruitment population is the most vulnerable and by dispersing them intelligently on available resources will have a repercussive ripple through the population which will suppress extreme population numbers in a habitat with density limitations.
2. Similar to the non age structured case, the age structured model delivered ESS's, CSS's and NIS's. It was seen that strategies that produced chaotic outcomes were CSS only.
3. An ESS is a strategy that is come by through a finite convergent series of stable strategies (CSS's). It also has the property that it is a neighborhood invader strategy (NIS) that will result in a positive growth spurge in the neighborhood populations when they are exposed to the ESS strategy instead of their own over (at least) one period.
4. The PIP graphs formulated in this study show that a CSS is visually a strategy associated with a vertical line passing through areas where the established

population cannot be replaced by any other neighborhood strategy generated population. A NIS is associated with a horizontal line passing through areas where the initially small population practicing the NIS strategy, will invade and replace an established population practicing another strategy. If these two lines cross for the same strategy and this crossing is a unique situation, such a strategy is known as an ESS. Recall that the horizontal axes represents an established population and the vertical axes represents an initially small population entering the environment.

5. From the real world cases it was seen that there are two ESS values, one for the constant case where environmental averages are used for the parameters defining the age-structure, and one for the case where a time varying parameter, chosen according to observed population tendencies, is incorporated into the defining parameters. Comparing these two ESS values indicate the impact environmental fluctuations have on a population's strategy. Alternatively, if an ESS generated population does not simulate the real world population, but another strategy does, then the difference in these two values can indicate the direction of evolution for this population.

Additional features of this study were:

1. Using the system coefficients to indicate certain types of periodic outcomes.
2. Linking the system coefficients of the age and stage structured models.
3. Incorporating a time variant growth rate parameter in the simulation of the real world cases where certain tendencies were observed.

Age-structure still has a lot to offer and one wonders what the outcomes will be if the Shepherd recruitment function is replaced by one of the other density functions such as the Hassel and the Cushing functions. The algorithm can easily be adapted to accommodate a different recruitment function as well as time variant parameters and is probably the most valuable outcome in this study.

Appendix A

Period Three and Chaos

Investigating the system requirements for the possible existence of a chaotic periodic point, will be based on the theorem of Li and Yorke which will briefly be discussed next [67]. The theorem is applicable to all continuous functions $F : R \rightarrow R$. It states that if F has a periodic point of prime period three, then F can have periodic points of all other periods as well, including chaos. Defining for the period three age structured model (3.103) the functions $H : R \rightarrow R$ and $\mathcal{G} : R \rightarrow R$ such that $H\{X(n)\} = X(n)((D^2 - EF)\psi(n) + E)$ and $\mathcal{G}\{X(n)\} = ((E^2 - DF)\psi(n) + D)X(n)$ then (3.103) can be written as:

$$\begin{aligned}
 X(n+2) &= \hat{\mathcal{R}}(u, \bar{X}(u))X(n) & (A.1) \\
 &= \frac{(E^2 - DF)\psi(n) + D}{(D^2 - EF)\psi(n+2) + E}X(n) \\
 X(n+2) \left((D^2 - EF)\psi(n+2) + E \right) &= \left((E^2 - DF)\psi(n) + D \right) X(n) \\
 H\{X(n+2)\} &= \mathcal{G}\{X(n)\} \\
 X(n+2) &= H^{-1}\{\mathcal{G}\{X(n)\}\} \\
 &= F\{X(n)\}
 \end{aligned}$$

Where $F\{\} = H^{-1}\{\mathcal{G}\{\}\}$. Note first of all that for $X(2) < X(1) < X(3)$, that

$$\begin{aligned}
 F\{X(2)\} &= X(1), & (A.2) \\
 F\{X(1)\} &= X(3), \\
 F\{X(3)\} &= X(2)
 \end{aligned}$$

Now define the intervals $J = [X(2) X(1)]$, $I = [X(1) X(3)]$ and $D = J \cup I$. The application of F on J will leave this interval and land in I , but application of F on I can either stay in this interval or land in J , that is,

$$I \subset F\{J\} \tag{A.3}$$

$$D \subset F\{I\} : \quad (\text{A.4})$$

$$\text{or } I \subset F\{I\} \quad (\text{A.5})$$

$$J \subset F\{I\} \quad (\text{A.6})$$

Two very useful lemmas follow from $E \subset F\{E\}$ and the continuity of F . They are the

1. *Fixed point lemma:* If E is a closed interval such that $E \subset F\{E\}$, then F has a fixed point in E . According to (A.5) there is a fixed point for F in I but not in J .
2. *Preimage lemma:* If E is a closed interval such that $E \subset F\{E\}$ then there exists a closed sub interval $e \subset E$ such that $E = F\{e\}$.

From (A.5) there is a closed subinterval $i_1 \subset I$ such that $I = F\{i_1\}$. From (A.5):

$$i_1 \subset I = F\{i_1\} \quad (\text{A.7})$$

$$\text{or rather } i_1 \subset F\{i_1\} \quad (\text{A.8})$$

showing a fixed point (prime period one) for F in $i_1 \subset I$. Extending the above search for fixed points, equation (A.13) and the preimage lemma shows that there must be a closed subset $i_2 \subset i_1$ such that $i_1 = F\{i_2\}$ so from (A.5)

$$i_2 \subset i_1 \subset I = F\{i_1\} = F^2\{i_2\} \quad (\text{A.9})$$

$$\text{or rather } i_2 \subset F^2\{i_2\} \quad (\text{A.10})$$

it follows from the fixed point lemma that F^2 has a fixed point in $i_2 \subset i_1 \subset I$. From (A.10) there must be a closed sub interval $i_3 \subset i_2$ such that $i_3 = F\{i_3\}$ but then again:

$$i_3 \subset i_2 \subset i_1 \subset I = F\{i_1\} = F^2\{i_2\} = F^3\{i_3\} \quad (\text{A.11})$$

$$\text{or rather } i_3 \subset F^3\{i_3\} \quad (\text{A.12})$$

showing a fixed point for F^3 in $i_3 \subset i_2 \subset i_1 \subset I$. It can be shown that for any k , F^k will have a fixed point in i_k where:

$$i_k \subset i_{k-1} \subset \dots \subset i_1 \subset I \quad (\text{A.13})$$

$$\text{and } I = F\{i_1\} = F^2\{i_2\} = \dots = F^k\{i_k\} \quad (\text{A.14})$$

This chain can at any stage be interrupted by (A.3) that shows by the preimage lemma that there must be a closed subset $j_0 \subset J$ such that from (A.13):

$$i_k \subset I \subset F\{J\} \quad (\text{A.15})$$

$$i_k = F\{j_0\} \quad (\text{A.16})$$

Then (A.14) will include J :

$$I = F\{i_1\} = F^2\{i_2\} = \dots = F^k\{i_k\} = F^{k+1}\{j_0\} \quad (\text{A.17})$$

From (A.10) and the fixed point lemma, letting $n = k + 2$:

$$j_0 \subset J \subset F\{I\} = F^n\{j_0\} \quad (\text{A.18})$$

there must be a fixed point for F^n in j_0 . On the other hand, (A.10) and the preimage lemma show that there must be a closed subinterval $i_m \subset I$ such that

$$\begin{aligned} j_0 &\subset J \subset F(I) \\ j_0 &= F\{i_m\} \end{aligned} \quad (\text{A.19})$$

then (A.17) shows that the following iterate will fall in I again:

$$I = F\{i_1\} = F^2\{i_2\} = \dots = F^k\{i_k\} = F^{k+1}\{j_0\} = F^{k+2}\{i_m\} \quad (\text{A.20})$$

From the fixed point lemma, the above shows that there is a fixed point for F^n in i_m . Since F visits J before spending the rest of its $n - 1$ iterates in I , it can be deduced that F has prime period n whether it starts in J or I .

Appendix B

The Stage-Structured Algorithm

The input and routines 1 and 2 of the age-structured algorithm is replaced by

1. Input:

$z7 = input$	Carrying capacity K of habitat	(B.1)
$mm = input$	the amount of age classes including juvenile	
$m = input$	stages excluding infant	
$stl = input$	stage lengths excluding juvenile stage : $[st_1 st_2 .. st_m]$	
$b = input$	vector with birth rates : $[b_1 b_2 .. b_m]$	
$f0 = input$	infant survival to age 1	
$fs = input$	survival rates : $[f_1 f_2 .. f_{m-1}]$	
$r = input$	population growth rate when densities are small	
$u = input$	first choice of v_i	
$h = 0.01$		
$f = 1$	adjustment to u_0 for next choice of u	
$M = input$	number of times (6.10) must be iterated with every new u	
$N = input$	period of periodic point tested for ESS	
$in = input$	value for X_{init}	

2. Routine 1: Calculating P_i 's and Q_i 's from the f_i 's:

$$\begin{aligned} & \text{for } i = 1 : m && \text{(B.2)} \\ & \quad a1 = 1 \\ & \quad \text{for } j = 1 : stl(i) - 1 \\ & \quad \quad a1 = a1 + (fs(i))^j \end{aligned}$$

$$\begin{aligned}
& \text{end} \\
P(i) &= ((fs(i))^{(stl(i))})/a1 \\
p(i) &= P(i)/fs(i) \\
Q(i) &= fs(i) - P(i) \\
q(i) &= Q(i)/fs(i) \\
& \text{end}
\end{aligned}$$

3. Routine 2: Iteration of difference equation (3.12) where X is the population iterated at u and $X1$ and $X2$ are what happens to X if strategies are switched:

(a) The stage-structure requires m initial values for $X, X1, X2$

$$\begin{aligned}
X(1) &= in && \text{total count of new born at time } n = 1 && \text{(B.3)} \\
X1(1) &= in \\
X2(1) &= in \\
\text{for } i &= 1 : m \\
x(ii, 1) &= in && \text{initial population in stage } ii \text{ at time } n = 1 \\
x1(ii, 1) &= in \\
x2(ii, 1) &= in \\
& \text{end}
\end{aligned}$$

(b) Switch X strategy u with slightly bigger $u1 = u + h$ and slightly smaller $u2 = u - h$

$$\begin{aligned}
& \text{for } i = 1 : M && \text{(B.4)} \\
P0(i) &= r/(1 + (X(i))^u) \\
P1(i) &= r/(1 + (X(i))^{u1}) \\
P2(i) &= r/(1 + (X(i))^{u2}) \\
x(1, i + 1) &= Q(1) * x(1, i) + f0 * P0(i) * X(i) && \text{juveniles in yearling stage} \\
x1(1, i + 1) &= Q(1) * x1(1, i) + f0 * P1(i) * X1(i) \\
x2(1, i + 1) &= Q(1) * x2(1, i) + f0 * P2(i) * X2(i) \\
& \text{for } j = 2 : m \\
x(j, i + 1) &= Q(j) * x(j, i) + P(j - 1) * x(j - 1, i) \\
x1(j, i + 1) &= Q(j) * x1(j, i) + P(j - 1) * x1(j - 1, i) \\
x2(j, i + 1) &= Q(j) * x2(j, i) + P(j - 1) * x2(j - 1, i) \\
& \text{end}
\end{aligned}$$

(c) Building the difference equations for the next juvenile generations

$$\begin{aligned}
 S_0 &= 0 & (B.5) \\
 S_1 &= 0 \\
 S_2 &= 0 \\
 \text{for } k &= 1 : m \\
 S_0 &= S_0 + b(k) * x(k, i + 1) \\
 S_1 &= S_1 + b(k) * x_1(k, i + 1) \\
 S_2 &= S_2 + b(k) * x_2(k, i + 1) \\
 \text{end} \\
 X(i + 1) &= S_0 \\
 X_1(i + 1) &= S_1 \\
 X_2(i + 1) &= S_2
 \end{aligned}$$

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ABSTRACT

In this study the evolution of the genetic composition of certain species will be replaced by the evolution of the traits that represent these genetic compositions. Depending on the nature of the trait of interest, a scalar valued parameter called the strategy parameter will be assigned to this trait making the simulation of strategy evolution possible. The trait of interest, and therefore the strategy associated, will be the ability of a population to keep its densities within the carrying capacity of the environment they find themselves in. The Shepherd function, on account of its wide use in population simulations as well as composing of exactly such a density parameter, will be the density curbing mechanism of choice in the age-structured population model designed here. An algorithm will be designed to simulate strategy evolution towards an evolutionary stable strategy or ESS that will ensure not only an optimal fit for this environment but also render the population immune against future invasion by other members of the population practising slight variations of this strategy. There are two ways to come by such an optimal strategy without directly involving genetics. The first is game theory, allowing strategists to compete for this position, and the second is with the use of adaptive dynamics, converting winning and losing instead into tangible mathematics. Combining these two classics will show that the quest is an exercise in strategy optimization, not only from the point of view of an already established population but also from the point of view of an initially small one. It will be interesting!

KEY TERMS

Density dependent models, Evolutionary game theory, Adaptive dynamics (AD), Fitness, Fitness function, Evolutionary stable strategy (ESS), Evolutionary steady strategy (EStS), Neighborhood invader strategy (NIS), Convergent stable strategy (CSS), Evolutionary singular strategy (ESiS), Shepherd function, Strategy optimization, Invasion exponent.

OPSOMMING

In hierdie studie word die evolusie van die genetiese samestellings verantwoordelik vir sekere karakteristieke van 'n spesies vervang deur die strategie wat hierdie karakteristieke verteenwoordig. As die strategie hom daartoe leen, kan dit as 'n skalaar verteenwoordig word wat die simulاسie van strategie evolusie moontlik maak. In hierdie studie is die strategie van belang die vermoë van die spesie om sy digtheid te reguleer binne die draagkrag van sy omgewing. As gevolg van die wye toepassing van die Shepherd funksie in populasie simulering en die teenwoordigheid van 'n strategie parameter, is dit die funksie van keuse in hierdie studie se ouderdoms gestruktureerde populasie model. 'n Algoritme word spesiaal vir die optimerings proses ontwerp wat die optimale strategie, ook genoem die evolusionere stabiele strategie of ESS, bereken deur die evolusie proses van die strategie te simuleer. Die implimentering van die ESS sal die populasie die voordeel bo ander gee wat 'n klein variasie van hierdie strategie beoefen. Beide spelteorie, waar populasies teen mekaar meding, en aanpassings-dinamika, wat wen en verloor wiskundig verteenwoordig, kan begruik word om die ESS te bepaal. Die kombinasie van die twee metodes wys dat die optimerings proses beide vanaf die ooppunt van 'n hoë digtheid asook 'n lae digtheid populasie kom.