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CO-EVOLUTION AND GENETIC ALGORITHMS

by

Jason Morrison, Hons.B.Sc., B.Eng.

A Thesis Submitted to
the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements
for the degree of Master of Computer Science

Ottawa-Carleton Institute for Computer Science

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in partial fulfillment of the requirements
for the degree of Master of Computer Science

Director, School of Computer Science

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September 16, 1997

For my father: Earl Edwin Morrison (June 15, 1943 - March 15, 1996)

“The difficult, we do now ... the impossible, takes a little longer.”

Thanks Dad.

Abstract

Genetic Algorithms (GAs) are a fast, efficient optimization technique capable of tackling many problems. Unfortunately the primary flaw of GAs is their constant drive toward a population containing a single local optima. This constant decay in the genetic diversity of the population decreases the GAs' capacity to find global optima and/or to adjust to changing objective functions. Recent advances in GAs indicate that the introduction of ecological models and the use of co-evolutionary architectures can slow or eliminate this loss of diversity. This thesis begins by surveying the full scope of previous work in GAs. It is the goal of this thesis to generalize the ecological models presented in these earlier works and to implement a GA which uses this to maintain its genetic diversity.

This goal is accomplished by the successful completion of several interconnected contributions. First by examining previous work in ecological and evolutionary modeling a consistent set of definitions, a graphical description technique and a classification scheme for ecological models are formulated. Following this a new formal mathematical model of evolving ecosystems is presented. This model is based on the definitions given here and is capable of expressing all forms of ecological models given in the classification scheme. In addition a description of the implementation of this mathematical model as a new flexible ecosystem extension to GAs is presented. Finally, it is shown that this implemented model is successful in keeping genetic diversity in a GA while often performing better optimizations.

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There are a number of people without whom I would not have started or completed this thesis. First among these people is my supervisor, Franz Oppacher. Through his vision and perseverance Evolutionary Computing and Artificial Life are actively researched at Carleton University. Without his influence my studies in this area would not have been possible. It was through Franz's suggestions that I began researching the area of co-evolution. I am grateful for both his suggestions and guidance. Most importantly, Franz has been patient with my mistakes and my very rough drafts. He often clarified and strengthened my work. Thank You Franz.

I would also like to acknowledge my friends and family for their support. All too often I would ramble on about a point they wouldn't care about, and still they offered their assistance, support and encouragement. I have valued each comment. Repeated thanks to everyone for making life enjoyable and easier through these studies.

With heartfelt gratitude I acknowledge those who over the years have answered my questions. It is to those teachers, friends and family members who patiently faced my curiosity that I owe my knowledge and abilities. Thank you.

Finally, this work is reliant on those mentioned in the references and upon the people mentioned above. Without these giants, this work would be mere supposition and I thank them for the solidity their shoulders have granted me.

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Chapter 1

Introduction

The topic of this thesis is the fusion of optimization problems with techniques observed in nature. The goal is to improve the previous natural-based optimization techniques (with specific interest in Genetic Algorithms). This goal is achieved through the development of a model called ‘The Symbiosis Model of Co-evolution’. Results show that this model of evolution, implemented in a Genetic Algorithm (GA), can eliminate the loss of genetic diversity normally experienced by a GA. Furthermore, it is shown that with this implementation, better or equivalent optimization is also achieved.

This chapter explains the basic concepts needed to understand the fusion of optimization problems with models of nature. The chapter then concludes by giving a description of the layout of this thesis.

1.1 Natural Selection and Evolution

Natural Selection is the process by which individuals in a system reproduce and die. It is a “Selection” because some individuals die young and others live long lives and because some individuals reproduce while others never get the chance.

This detached view leads to the thought that Natural Selection is the mechanism by which Evolution occurs. “Evolution” can be defined as the change in the individuals of a population (through reproduction or otherwise) that occurs because of Natural Selection. Thus if small individuals die before large individuals then large individuals will reproduce and the average member of the population will become larger.

Natural Selection acts upon individuals. The definition of an individual is a difficult but it is the opinion of the author that three properties should be included.

- Individuals usually die.
- Individuals tend to reproduce.
- Individuals interact constantly (e.g. hurting, stealing, aiding, using, feeding, teaching, protecting, mating with, killing, ...)

The first two properties are the foundations for the concept of fitness discussed in the next section. The third property is the topic of this thesis.

1.2 Fitness

Critical to any model of natural selection is the concept of an individual's fitness. It is uncertain who originated the idea that an individual has an intrinsic fitness. It seems to trace its root back to the phrase “Survival of the Fittest” which was used interchangeably with “Natural Selection” in Herbert Spencer's *Principles of Biology*(1864)¹. Worse than trying to trace the history of the word ‘fitness’ is trying to trace the meaning of the word. While there is no accepted definition of fitness[5] there are some fundamental consistencies presented in other definitions [5, 19] that the definition presented here tries to include.

¹A more complete history on the concept of fitness is given in Diane Paul's work “Fitness: Historical Perspective”[49].

Fitness has two components, the ability of an individual to survive and the ability of an individual to reproduce. Each of these components will be considered a separate fitness described by Definitions 1.1 and 1.2.

Definition 1.1 *An individual's Survival Fitness, at time t , is the probability that the individual will survive until time $t + 1$.*

Definition 1.2 *An individual's Reproductive Fitness, at time t , is the probability that the individual will reproduce before time $t + 1$.²*

The increment used in making time a discrete entity is not specified to allow flexibility within the definition.

There are disagreements regarding how the two fitnesses defined above combine to create an individual's overall fitness. In a model of nature an individual's fitness should be the basis for Natural Selection. Thus the selection of which individuals breed and which survive is determined by the individuals' overall fitnesses. A complex function to summarize the fitness of an individual could be derived using the number of progeny, successors and/or the length of an individual's life but there is a simpler way:

Definition 1.3 *An individual's Overall Fitness at time t is the vector of the individual's survival and reproductive fitnesses at time t .*

Before discussing the ramifications of this definition of fitness there are two terms that need to be defined. The first definition defines the term 'factor' as it relates to the fitness of an individual. The second defines an "environment" and how it relates to an individual and its fitness.

Definition 1.4 *A Fitness Factor, of an individual, is anything which, when altered, can produce a change in the fitness of an individual.*

²It is assumed here that "reproduce" means that offspring will be born between times t and $t + 1$.

Definition 1.5 *An individual's Environment is the collection of all fitness factors³ of the individual that are not individuals.*

The definition of fitness, given above, provides a measure of an individual at an instant in time. This is better than the approach where the fitness of an individual depends on the number of its successors because such a fitness is dependent on all the fitness factors of all the successors. Instead this new fitness depends only on the individual's fitness factors.

The usage of the word 'fitness' in this thesis must be viewed within the context mentioned, either the survival fitness or reproductive fitness or both may be referred to when 'fitness' is mentioned. In much of the literature the survival fitness and reproductive fitness are based on a single function⁴. Since, in this case, the components are co-related they are often mentioned as one fitness.

1.2.1 Related Terminology

There are several terms that are used throughout this thesis that deal with evolution and the nature of evolution. The most commonly used term amongst these is "genome". Essentially the genome of an individual is all of the genetic material that the individual uses to reproduce.

Only two other undefined evolutionary terms reappear throughout the work. The first of these terms is 'genotype' which refers to the group of individuals containing compatible genomes (i.e., a species) or it refers to the form of said genomes. The second term is 'phenotype' which refers to the visible characteristics of an individual that are produced by the interaction of the individual's genome and the environment.⁵

³see Definition 1.4

⁴GAs are often an example of this.

⁵Adapted from the Merriam-Webster online dictionary

1.3 Evolution vs. Evolutionary Computing

Evolution, as previously mentioned, is the process resulting from natural selection. Since natural selection can be defined this implies that it can be modeled and hence evolution can be modeled. This is interesting because evolution tends to form intricate yet robust systems in order to survive. A brief example would be the social behaviour of ants: each ant acts on a local scale, following minimal rules and yet collectively the ants are able to behave as intelligent pathfinders and gatherers.

Evolutionary Computing (EC) is a set of computational techniques that try to use models of natural selection to evolve solutions to problems. It is the goal of EC to have a system create the solutions to a problem where the system itself generates the exact form of the solutions. It is another goal of EC to have systems that create solutions with as little knowledge of the problem as possible. Introductory surveys of the techniques used in EC are available in [24, 43].

Briefly, the idea of EC is to maintain a population of individuals where each individual represents a potential solution to a problem. Since each individual is a potential solution to a problem then, for EC to work, there must exist a measure of how well the solution solves the problem. This measure is called the ‘fitness’ of the individual and is used to determine the reproductive fitness and survival fitness of the individual. With each round the reproductive fitness is used to select which individuals breed to create new individuals (i.e., new solutions). Then the selective fitness is used to determine who survives into the following round. The processes of reproduction and selection are repeated with each of these rounds referred to as a “generation”. Since the selective and reproductive fitnesses favour better solutions, with every generation, the population gets better and better at solving the problem.

Selection for survival and reproduction is usually probabilistic. Most reproduction itself usually involves some degree of randomness as well. This leads to a discussion on the efficiency of EC versus deterministic techniques. One application of EC is in solving optimization problems where nothing is known except the form of the input. In these problems it takes an examination of every possible input to

determine which input is the actual optimum. These NP complete problems are typically too large to try such an exhaustive approach, so heuristic techniques are often used. Unfortunately heuristic techniques often stop long before finding an optimum and do not continually search the input space. EC techniques are an attempt to circumvent this problem of premature convergence in a directed heuristic. While they are not successful on all problems there are a wide number of problems that they are quite good at solving [13].

1.4 Genetic Algorithms

Genetic Algorithms (GAs) are just a portion of the techniques of EC. There are many variations of GAs that occur within the literature: however, the version presented here represents what will be coined a “regular GA” for the rest of this thesis. This does not imply that the specific type discussed here is the only type used; but it is the most thoroughly examined in the GA literature⁶.

It is assumed that there is a function f for which a maximal value f_{max} is desired. It is also assumed that some individual X_{max} exists such that $f_{max} = f(X_{max})$. The GA begins by randomly creating a population of N individuals $P_0 = \{X_{(1,0)}, \dots, X_{(i,0)}, \dots, X_{(N,0)}\}$. Each of the individuals are given a fitness of $f(X_{(i,t)})$. It is assumed that no member of a population will survive longer than one generation (i.e., the survival fitness of all individuals is 0). However the choice of reproductive fitness (see Definition 1.2) is based on the fitness $f(X_{(i,t)})$. The probability of individual X_i at time t reproducing is given in Equation 1.1.

$$P(X_{(i,t)}) = \frac{f(X_{(i,t)})}{\sum_{j=1}^N f(X_{(j,t)})} \quad (1.1)$$

Pairs of individuals are chosen according the the probabilities described by Equation 1.1 and a reproduction operator Φ is used⁷ to produce children $X_{(i,t+1)} =$

⁶Goldberg in [13] refers to this form of GA as the Simple GA.

⁷This method of reproduction might be the mutation of one individual's genome to produce a child or the combination of both individuals' genomes or it could be a probabilistic choice between

$\Phi(X_{(j,t)}, X_{(k,t)})$. N children are produced in this fashion and they replace the old population. The process is then repeated with the new generation. Either the process stops after some number of iterations have passed or when the entire population is full of identical individuals.

While there are different variations of reproduction operators, different schemes for deciding the reproductive fitness and the survival fitness of individuals the core idea of a single population GA is expressed in the regular GA described above. For further explanations the reader should see [13, 19].

1.5 Thesis Organization

The remainder of this thesis has been broken down into five parts. In Chapter 2 previous work in co-evolutionary GA's is described, the goals of this thesis are given and their implications are examined.

In Chapter 3 definitions relevant to co-evolution are discussed and a graphical technique of modeling interactions is introduced. The chapter continues with the discussion of feedback as it relates to co-evolution and the categories of co-evolution are defined.

Chapter 4 discusses models of co-evolution beginning with related work. The introduction of a new model of co-evolution is given and a mathematical framework for co-evolution is established. This model is then extended and specific properties of the extended model are formulated.

In Chapter 5 the implementation of the new model is discussed. An object model of the implementation is given and the forms of co-evolution that were studied are described. Following this is a description of the parameters of the implemented Genetic Algorithm.

With Chapter 6 a full description of the problems and genomes used during experimentation is given. This is followed by the description of the experiments performed and a discussion of results obtained.

the two. Only creativity and the form of the individuals has limited these operators.

Finally the conclusions note the contributions of this work and discuss the future work possible in the field.

Chapter 2

Previous Work, Goals and their Implications

The source of motivation for this thesis is a small but growing body of work in Genetic Algorithms (GAs). Collectively named co-evolution by its researchers and proponents the field has shown excellent results. Unfortunately the definition of what is and what is not co-evolutionary is unclear. No definitions have been given and surveys of work are brief sections in papers. Nor is it clear whether co-evolution, as represented by these works, is analogous to co-evolution as defined in biological and ecological research. An examination of the works in the field provides the necessary background to form a consistent set of definitions applicable to this and future work.

Before describing the previous works in GAs it is appropriate to mention the related works in Artificial Life, Genetic Programming and Classifier Systems. All of these fields have many instances of co-evolution consistent with the work provided here. A survey of all such research is beyond the scope of this thesis. However, there are some papers in the field of Artificial Life that the reader might find interesting. These papers [11, 23, 25, 34, 35, 42, 45, 54] range in topics from the use of co-evolution as a basis for a new form of Evolutionary Computation [11] to the simulation of ecosystems [54].

2.1 Previous Work in Genetic Algorithms

Within Evolutionary Computation the area of co-evolution is inadequately explored. While the area of co-evolution is growing, it is often overlooked and under-appreciated. In Michalewicz's 1994 paper "A Perspective on Evolutionary Computation" [43], co-evolutionary techniques get one paragraph and only one reference. Reynolds paper "Competition, Co-evolution and the Game of Tag" [56] although not entirely relevant to this discussion because it uses Genetic Programming, contains one of the few surveys of related work. To the best of the author's knowledge it is, outside of this thesis, the largest survey on co-evolution in GAs. During the review of relevant literature only four main types of GAs were found that were described as being co-evolutionary. All of the following works are admitted to this section because they present reasonable arguments defining themselves as being co-evolutionary in nature.

2.1.1 Competitive Fitness Functions

Most of the examples of co-evolution in GAs fall into the category of competitive fitness functions. Angeline and Pollack's paper "Competitive Environments Evolve Better Solutions for Complex Tasks" [1] defines competitive fitness functions to be "any calculation for fitness that is dependent on the current population to any degree"[1. p. 265]¹. The paper continues to cite two relevant papers in the GA literature.

The first of the two is Axelrod's paper "Evolution of Strategies in the Iterated Prisoner's Dilemma" [3]. A proponent of Evolutionary Game Theory (see Section 4.1.2), Axelrod had previously written the book "The Evolution of Cooperation" [2] which studies the Iterated Prisoner's Dilemma (IPD). Like the Hawk-Dove model, presented in Section 4.1.2, the IPD is a two person game where each person has two

¹By this definition of competitive fitness functions they are not necessarily competitive. However, this terminology will be used whenever the definition given applies.

possible behaviours. Each person repeatedly plays against the same person and uses some mixture of behaviours to try and maximize their payoffs.

Axelrod's goal in his 1989 paper was to study what strategies emerge from an evolving population of individuals that play IPD games. Axelrod used a GA to evolve a set of players whose fitnesses were evaluated by conducting a round robin tournament and used the resultant payoffs to each individual as their fitness.

The second paper mentioned by Angeline and Pollack was written in 1991 by Hillis. In his paper "Co-evolving Parasites Improve Simulated Evolution as an Optimized Procedure" [17] Hillis incorrectly associates his form of co-evolution to predation (i.e., Parasite-Host) when it is actually competition (i.e., Competitor-Competitor). Hillis created two populations to be manipulated by two GAs. In the first population, individuals were parallel sorting networks and in the second population, individuals were groups of test cases to be sorted. Every individual in the first population was paired with an individual in the second population and the pairs then competed for fitness. The sorting network would get a unit of fitness for every test case it could sort. An individual consisting of test cases received a unit of fitness every time a sorting network failed to sort one of its test cases. The co-evolution studied by Hillis produced more accurate results than a corresponding evolutionary approach and was significantly faster.

Despite the relative popularity of competitive fitness functions there exists a problem that is rarely dealt with. This problem is exhibited, in its simplest form, in the following example. A system contains individuals with three possible behaviours (a, b and c). Each individual in the population can exhibit only one of the behaviours throughout its life. This implies that there are three types of individuals A, B and C each exhibiting behaviours a, b and c respectively. Individuals compete for resources in a pairwise fashion. The proportions of the resource that the individuals receive is based on the behaviour of the individuals that are competing. It is assumed that when two individuals compete that are of the same type they share the resource equally.

Suppose that when two individuals compete, one of type A and another of type

B. type A always obtains more of the resource than type B. Then type A will begin to dominate the environment. Suppose that individuals of type C are introduced into the population and that when types A and C compete for a resource they share the resource equally. This means that type C can invade the environment and share it with type A.

Consider what happens if type B individuals take the majority of a resource when they compete with type C individuals. If individuals of type B are introduced to the A and C mixture then evolutionary cycling can occur. That is the population will fluctuate from (A's and B's) to (A's) to (A's and C's) to (A's and B's) again (see Figure 2.1). It has been demonstrated [42, p. 163] that IPD, implemented in a GA, contains such behaviours and therefore can exhibit evolutionary cycling.

Darwen and Yao used Axelrod's paper and explored the differences between competitive fitness functions and fixed fitness functions on the IPD[72]. It was their hope to eliminate evolutionary cycling because it often produces sub-optimal results². Their conclusion was that it is best to mix the fitness function so that an individual's fitness is determined by competition with both a fixed group of individuals and a group of the current population³.

Darwen and Yao continued the use of competitive fitness functions with their work on the NIPD (n-person Iterated Prisoner's Dilemma)[73]. This problem, while less explored than the IPD, is "more realistic"[73, p. 91] in its exploration of social and economic problems. Using a single population of 100 individuals, Darwen and Yao evolved players by conducting 1000 games of the NIPD. Since the NIPD game is not well studied the objective of the research was to see how it differed from the IPD. They concluded that it was less likely that cooperation would develop in larger problem sizes and they did not mention problems of co-evolutionary cycling.

Using the work of Hillis[17] as a template, Paredis adapted the scheme and

²It is desirable to eliminate evolutionary cycling from a system only when a higher fitness is desired. When natural behaviour is desired then

³Darwen and Yao did not categorize the evolutionary cycling as clearly as was done here. This categorization is due to insights provided in [42] and its projection onto Darwen and Yao's paper [72].

Figure 2.1: Evolutionary Cycling occurs in this system because the system is “attracted” to the states shown with circles. Admittedly not all configurations are shown but the essence of the cycling is captured here. At any state the proportions of the behaviours in the populations will drive it toward one of the attractors. The arrows indicate the direction the system is driven to if it were at the attractors.

applied his adaptation to two problems[46, 47]. Paredis' adaptation was that he did not keep two dynamic GAs. Instead he kept one population of solutions maintained by a GA and another population of test cases that were ranked by fitness and evaluated, but never reproduced or mutated. The fitness of the solutions was a rating of how well they solved the test cases they were presented with. The fitness of the test cases was based on how well they stumped the solutions. Solutions were tested against test cases on a random basis with the test cases having higher fitnesses being selected 1.5 times more often than the median. Reproduction of one new solution occurred after a specified number of test cases had been tested.

Paredis obtained very good results in applying his adaptation to both Constraint Satisfaction Problems[46] and Neural Net Classification Problems[47]. He compared the results of his co-evolutionary techniques to a regular GA that used all of the test cases to determine the fitness of individuals. In both cases the solutions produced were better and fewer test cases were evaluated.

In "Constraints on Task and Search Complexity in GA + NN Models of Learning and Adaptive Behaviour" Patel provides another instance of competitive⁴ fitness functions[48]. In this work Patel details a method of using GA's to develop controllers that control agents that play soccer. This game of soccer was with two agents on one team and no agents on the opposing team⁵. Individuals were awarded fitness for passing to the partner, shooting or moving the ball toward the goal. Since there were two players involved at any one time both players received the same fitness. Thus the system employs cooperation between individuals and is an example of co-evolution. Most important to this research is the success of the players: goals were scored, passes were made and a good time was had by all.

The final and most interesting use of the competitive fitness function was by Sims in "Evolving 3D Morphology and Behavior by Competition"[61]. Sims specified a new crossover operator that reproduces the genotype of his system. The genotype

⁴This is one case where the 'competitive' fitness function is not truly competitive. It is actually co-operative but meets the definition of a competitive fitness function set by Angeline and Pollack.

⁵Patel claims in the paper that the two on two version was too computationally intensive with existing equipment.

was a graph representation of a individual's body structure including joints, motor systems, sensors and control structures. Each individual was evaluated by placing it in competition with another individual in a simulated ring. Each competition was a simulation of a 3D environment with mass, gravity and friction where both individuals start equidistant from a box. After the simulation of a fixed time interval the fitness of each individual was calculated by its distance to the box compared to its opponent's distance to the box.

The success of Sims' "creatures" is astonishing. Not only do creatures find the box but several of them learned to pin down the opponent. Still others learn that moving the box is a winning strategy. Sims mentions that the best competition was between a large creature that walked away with the box and a photosensitive arm that kept after the box[61, p. 36].

It is uncertain if a hand-crafted individual could beat one of the creatures that Sims evolved. What is certain is that Sims did not have to try and program the wide variety of behaviours exhibited by his evolved creatures. Forcing individuals to compete and deciding survival and reproductive fitness on the results of that competition allowed the system to evolve successful behaviours without outside influence⁶. It is work like this that approaches satisfying the goals of Evolutionary Computing.

2.1.2 Niche and Species Methods

Niche and Species methods in GAs did not begin as an attempt to model co-evolution. Using the GA, defined by Holland[19], the population loses genetic diversity with each generation. The original purpose of Niche and Species methods was to counteract this effect[9]. In attempting to create biological analogies the researchers created some of the first co-evolutionary extensions to GAs. To the best of the author's knowledge, Davidor[9] is the first to acknowledge these techniques as co-evolutionary and argues his point effectively.

⁶Sims' does not mention his degree of involvement but it is assumed to be minimal given the context of the paper.

Deb and Goldberg are the authors of “An Investigation of Niche and Species Formation in Genetic Function Optimization”[10] which is an excellent paper covering the definitions and execution of the Niche and Species methods. Two popular methods covered in this paper are the using of sharing and crowding functions. While Deb and Goldberg cover variations on these two types of functions it is only necessary to present their general concepts in this work.

A sharing function is an expressed fitness function which is equal to or less than an individual's absolute fitness. A specific individual's evaluation depend on how many individuals it is phenotypically or genetically close to in the population⁷. The more individuals that the evaluated individual is close to the lower its expressed fitness. In a crowding function, an individual's survival fitness is wholly determined by competition. The crowding factor CF is defined as the number of individuals randomly chosen to decide where a new offspring is to be located. With the birth of a new individual CF individuals are selected and the individual that is genetically most similar to the new offspring is eliminated. It can be argued that both Crowding and Sharing are methods of local competition because the concept of injury (or death) due to space limitations has been implemented. One of the best advantages of Sharing and Crowding is their ability to find multiple global optima.

Davidor presented a new technique within the realm of niche and species methods in his paper “A Naturally Occurring Niche & Species Phenomenon: The Model and First Results”[9]. Before presenting his model, Davidor reviews the previous Niche and Species work, including some work not relevant to a discussion of GA techniques. Davidor then presents contribution to co-evolutionary GAs called: The ECO GA. Essentially this is a GA where each individual is placed on a toroidal grid (i.e., the opposite edges of the grid are connected and each cell in the grid has eight neighbours). Every 3 by 3 sub grid is considered a population and two individuals are selected to breed creating one new individual. This new individual is placed in one of the nine cells in its population. Since there is already another individual in

⁷The phrase “phenotypically or genetically close to” is general to cover the range of sharing functions. For more detail see [10].

this cell they must compete for the space. The competition is probabilistic based on the relative fitnesses of individuals within the cell.

Because of the competition for space, Davidor's ECO system is co-evolutionary. In his analysis of the system he shows that the fitnesses of individuals converge "more quickly as the search progresses" [9, p. 259]. In this initial work Davidor's conclusions are promising but does not make a comparison to regular GAs.

It could be argued that the nature of competitive selection in these algorithms is not substantially different from a regular GA. If the above works are not different from the regular GA then it is implied that the regular GA is co-evolutionary. There does exist one major difference between the Niche and Species methods and the regular GA. When the fitness-proportionate selection of Regular GAs is used, all individuals are affected in the same manner. Selection probability is determined by the ratio of an individual's fitness over the sum of the fitness of all other individuals. In the Niche and Species methods selection probability (i.e., co-evolutionary fitness) is determined by a subpopulation and does not have an equal effect on all individuals. Whether this difference negates the implication that Regular GAs are co-evolutionary can still be debated and the author's position is discussed in Section 2.2.

2.1.3 Multiple Population Approaches

Typically, co-evolution is thought of as a multi-population phenomenon. Different species are thought to affect each other's fitness and thereby change which individuals are selected. By influencing the process of natural selection, the relationship between species, changes the evolution of the system. This alternate form of evolution is commonly thought of as co-evolution.

It is the multiple population form of co-evolution that was implemented by Potter and DeJong in "A Cooperative Co-evolutionary Approach to Function Optimization" [53]. In their approach, when a given solution has n components then n different populations of components are co-evolved. Potter and DeJong defined the fitness of an individual to be the fitness obtained by its composition with a member from the

remaining $n - 1$ species. Since the individuals are tested together, suffer or thrive together then the individuals are symbionts. This type of mutualism formed between symbionts is co-evolutionary and is the defining component of co-evolution within the system. Unfortunately their paper did not explain how the individuals are chosen for composition; but, excellent results are reported on optimizing vector functions. In the cases presented by Potter and DeJong, each population represented one component of a solution vector. Each individual's fitness was determined by taking one individual from each population to compose a vector X . This vector was used in the vector function (f) being optimized and each individual member of the vector was given the evaluation of the function $f(X)$ as its fitness.

Husbands and Mill published an interesting approach to co-evolution that uses a mixture of both multiple population techniques and competitive fitness functions. Their paper "Simulated Co-Evolution as The Mechanism for Emergent Planning and Scheduling"[21] deals with the complex issue of task scheduling in a machine shop environment. Their approach to the problem is general enough to deal with many scheduling problems but the terminology used here reflects that used in the paper. Husbands and Mill began with $n + 1$ populations, one for each of the n parts that are to be made and one population of Arbitrators. Each of the n part populations consisted of a set of individuals that were process plans to make the part. Such a process plan contained a list of steps and each step indicated the operation, machine and setup to be performed. Fitness of individuals was evaluated by taking individuals from every population and simulating the machine shop.

In the simulated machine shop, the process plans of the different individuals were executed. Whenever a conflict arose because two or more parts required a specific machine at the same time, the Arbitrator decided the outcome. The fitness of an individual was the inverse of the total time spent to make the part (i.e., the shorter the time to make the part the better the fitness). Similarly the fitness of the Arbitrator was the inverse of the length of time to make all parts. Since the Arbitrator benefited when time went down as did the parts there was mutualism between the Arbitrator and individuals of part populations. However, there was

competition between individuals of different part populations. The result of these symbioses is a co-evolutionary system that reduces the amount of time required to make all of the parts (the authors quote an example where there is a 60% reduction in total time to make all parts).

Pham investigated another form of co-evolution using multiple populations in his paper: “Competitive Evolution: A Natural Approach to Operator Selection” [51]. In his approach p populations are initialized. Each of these populations uses a different technique (i.e., a different mutation rate, or a different crossover operator,...). The algorithm begins by choosing two populations: the population with the fittest member and the population that has stalled the least (i.e., most recently produced fitter offspring). These two populations are then evolved for a specified number of steps and the algorithm is repeated until a stopping condition is met. The co-evolution in Pham’s system is not easy to see. Individuals in a population compete with individuals in other populations for the right to breed. Thus as the fitness of individuals increases in one population its opponents in other populations suffer. This means that all populations are in direct competition with each other. Thus co-evolution exists in the system.

2.1.4 Artificial Symbiogenesis

Bull and Fogarty’s paper “Artificial Symbiogenesis” [7] is unique for two reasons: the use of the NKC Fitness Landscape (See Section 4.1.3) with GAs and the use of a co-evolutionary GA to explore the behaviour of co-evolution. In this work Bull and Fogarty model the hypothesis of endosymbiosis which they define as “the hypothesis that if the relationship between symbionts evolves in the direction of increasing dependency, potentially a new formation at the level of the organism arises – a complex form having the attributes of an integrated morphophysiological entity” [7, p. 229]. This means that they were modeling the cooperation between individuals that results in the two individuals becoming one. The paper gives an excellent introduction to the relevant evolutionary biology and then proceeds with the construction of the model.

The model itself uses the GA as a simulation tool for evolution in place of Kauffman and Johnsen's mutation technique (See Section 4.1.3). While this does not represent an advance in the field of Evolutionary Computation it does represent an advance in Evolutionary Studies. Bull and Fogarty were able to analyze the system in terms of gene transfer between individuals and the conditions necessary for endosymbiosis to evolve instead of simple cooperation. Fogarty's work continues to show that the GA community can provide useful insights into the behaviour of evolution in natural systems.

2.2 Motivation, Goals and Implications

In almost every example the co-evolutionary GA either performed better than a regular GA or it performed an optimization that was not possible with a regular GA. While these claims did not imply that co-evolution was always better, they do imply that the possibility of unexplored improvement exists. This hint of opportunity was the prime motivation for this work. Given this motivation a set of goals was drawn up for this research.

Exploration into co-evolution led to three specific goals for this research:

- I Researching co-evolution has provided the possibility to incorporate new evolutionary processes into GAs. This should be a general extension of GAs with the purpose of accurately representing as many different forms of co-evolution as possible.
- II In achieving the goal stated in I, it is hoped that the model created will produce a more efficient GA. This translates into two objectives: i) the loss of genetic diversity in a normal GA should not occur in the co-evolutionary system and ii) the co-evolutionary system should be able to produce better solutions (i.e., closer to optimal solutions).
- III Keeping in mind that goals I and II are most important, the model developed should be a model of co-evolution unto itself having as little dependence on

GAs as possible. It should offer mathematical precision and be consistent, wherever possible, with previous models and terminology of co-evolution.

The only major conflict between the three goals listed above was that Lewis' definition of symbiosis [33] was modified to include relationships between individuals of the same species. This was done to be consistent with the idea that co-evolution can occur within a species. In a biological context this amounts to defining social behaviour within a species as being a form of symbiosis⁸.

Given these goals, no haphazard definition of co-evolution will suffice. The definition must conform to the previous work in GAs, and it must conform to conventions and terminology of previous models in biology. Thus trying to accomplish these goals implies certain facts about the system.

One of the most important facts implied by the previous work is that a single population system can co-evolve. This raises the question "What systems are co-evolutionary?". Within common usage the term 'co-evolution' means the form of evolution occurring when two populations interact. A definition based on this idea would not include many GAs already considered to be co-evolutionary. In view of the goals, this is not an acceptable definition.

The approach that is taken here in creating the definition of co-evolution looks at the basic processes that are common to the previous co-evolutionary research. In this approach, co-evolution is defined by the presence of Natural Selection, on a group of individuals, whose fitnesses are interdependent. As previously stated this is a broad definition and may include the regular GA.

The reproduction selection operator⁹ in the regular GA uses the fitness of an individual and divides by the total fitness of all individuals. Thus an individual's reproductive fitness, as defined in Definition 1.2, is affected by all individuals. By the informal definition given here and by the formal definitions given in Chapter 3 this is a form of co-evolution. An individual's reproductive fitness is being affected

⁸The usage of 'symbiosis' here is not the common usage. The definition, as used here, is given in the next chapter.

⁹The operator discussed here is fitness proportionate selection.

by the other members of the population and thus there is competition within the population. However, it is the author's opinion that the regular GA is an uninteresting form of co-evolution. The reason for this opinion is that every individual's fitness is affected by the entire population in the uniform a manner. This fixed and inflexible manner of calculating reproductive fitness only represents one type of co-evolution.

Since the regular GA is considered a co-evolutionary system, in name if not in behaviour, then there are many adaptations of the regular GA that could also be considered co-evolutionary. Here the author issues a clear warning not to refer to everything as simply co-evolutionary. While it is within the bounds of co-evolution it is better to categorize co-evolution and discuss any particular GA or GA extension by those categories. In this fashion a systematic study of the behaviour of co-evolutionary systems within GAs can be performed. Toward this goal the following categorization is given:

- Any system directly modeled on a biological system, exhibiting co-evolution, should be classified by the type of co-evolution it is modeling. Any system that is capable of modeling multiple forms of co-evolution should be considered a separate category¹⁰.
- Systems that correspond to the previous research should be classified as co-evolutionary according to the category or categories described above.
- A GA system that is not categorized by the above definitions, but corresponds to the definition of co-evolution, should be described as unintentional co-evolution.

If these categorizations are defined by types of co-evolution found in nature , then clear definitions of these different types are required. Unfortunately, in biology there are more than one set of classifications. To avoid confusion one consistent set

¹⁰One such system, The Linear Symbiosis Model of Co-evolution, is presented in this thesis. (see Section 4.2.2)

of definitions should be used. The next chapter is an endeavor to provide a set of such definitions.

Chapter 3

Definitions of Co-evolution

3.1 Introduction

Co-evolution refers to the evolution of multiple species that affect one another. As one species evolves it changes the relationship it has with surrounding species. If the hare species evolves faster legs then the fox species must live with less food or develop more cunning. While this is not a precise definition, this perception of co-evolution is a good beginning. In the study of ecology there are abundant examples of intertwined species [15, 16, 29, 62, 66, 71]. In truth this idea of co-evolution seems redundant because there are no examples of a species evolving by itself¹. However, evolution of a species could theoretically be independent of all other species. It is this independent model that has been used as the original basis for GAs. Only recently has experimentation begun with co-evolutionary implementations.

Before any discussion of the varying implementations, a clear understanding of how species are intertwined is critical. What does it mean to say that the fox and hare populations are intertwined? Fortunately ecological studies provide a systematic set of definitions and categories based on the idea of symbiosis.

In 1879 deBary defined the word symbiosis to mean “... Zusammenlebens ungleichnamiger Organismen ...” or “...the living together of differently named organisms

¹The author challenges the reader to find an antisocial species, which consumes no living creature and is not the predator or prey of any other species. It is noteworthy that even such a creature may still be co-evolving through commensalism.

...” [14]. As with most words, ‘symbiosis’ has come to have many technical and common usages. The most common usage is that two things are in symbiosis when they are interdependent and both derive benefit from the relationship. This layman’s view of symbiosis has its proponents in the technical world; however, there is a split amongst experts as to what the precise definition of symbiosis should be. Debates rage as to whether deBary’s definition of symbiosis should be taken literally or not, even whether it should be abandoned.

Definition 3.1 (after [33]) leads to a clear categorization of all possible intertwining of species that are involved in co-evolution.

Definition 3.1 *Symbiosis is defined by a relationship between two individuals where the fitness of one individual directly affects the fitness of the other individual.*

Quite frankly this definition appears general because it is intended to be used in a broad context. It is important to stress that the fitness referred to in this definition of symbiosis, is the overall fitness (see Section 1.2) of an individual. If an individual changes either the survival fitness or reproductive fitness of another individual then the relationship between them is symbiotic. For example a tick is in symbiosis with the dog it lives on and a herd of gazelles is in symbiosis with the pack of hyenas hunting it.

It is a common mistake to think that a symbiosis exists between a non-living dynamic factor (see Definition 1.4) and an individual. An excellent example is a fish and the river it lives in. The fish is not in symbiosis with the river it lives in. The river may affect the fitness of the fish but a symbiosis only exists when the river is changing because of another individual (or group of individuals). Specifically, if a beaver dams the river upstream then the fish is in symbiosis with the beaver.

Expounding the example of the beaver gives a clearer notion of what it means to “directly affect” an individual’s fitness. Since the beaver is controlling the environment of the fish and thus affects the survival fitness of the fish then the beaver and the fish are in symbiosis. While the beaver is controlling the fitness of the fish

through its effect on the river, the beaver is still deemed as directly affecting the fish because there is no intermediate individual.

For an example of an indirect effect, consider that a hyena is in symbiosis with any giraffes it hunts. In turn the giraffes are in symbiosis with the trees they eat. Since the hyenas do not directly affect the trees² nor vice versa, then the hyenas are not in symbiosis with these trees. Yet the argument can be made that the hyena may affect the survival fitness of a giraffe and since the giraffe affects the survival fitness of the tree then the hyena indirectly affects the tree.

Another false assumption regarding this definition of symbiosis is that it is a relationship between species. Using this definition, symbiosis is between two individuals. There is no singular symbiosis between ticks and dogs. There are symbioses between particular ticks and dogs. As another example all gazelles and hyenas are not in symbiosis. However, symbioses do exist between those hyenas that hunt and the particular gazelles that they chase (and/or kill). It is also important to note that individuals within a species are often in symbiosis with each other. Parents feeding children, pack hunting and mating competitions are all examples of symbiosis within a species. This extends deBary's definition of symbiosis by ignoring the constraint that the individuals be from different species.

Finally the non-persistent nature of some symbioses is important. When an individual is affected just once it has been affected. Consider that people who are most vulnerable to the German Mumps can become sterile. While the relationship between the human and the virus may be temporary it has drastically affected the reproductive fitness of the person and must be classified as a symbiotic relationship.

Using Definition 3.1 it is possible to formally define co-evolution.

Definition 3.2 *Co-evolution of a population with itself occurs when individuals within the population are in symbiosis with other individuals in the same population. Co-evolution of a pair of populations with each other occurs when individuals in one population are in symbiosis with individuals of the other population.*

²this is an assumption made for the sake of the example

Thus co-evolution occurs only when symbiosis is present. In fact in the presence of symbiosis natural selection, produces co-evolution. Without symbiotic relationships present individuals strictly evolve they do not co-evolve.

The previous definitions are almost complete enough to build and examine a model of co-evolution. The missing clarification is shown by the vague sense that an individual is affected by another individual. A sense of connection is conveyed by the association of two individuals and it is this “connection” that escapes description and is necessarily defined in the next section.

3.1.1 Connections

Ambiguities quickly arise when considering the statement “the parent is in symbiosis with its child”. This statement simply describes that the symbiosis exists, it says nothing about the nature of the symbiosis. It is not clear from the definition of symbiosis (see Definition 3.1) whether the child affects the parent’s fitness and/or the parent affects the child’s fitness. Nor does the statement describe how the fitness(es) are affected.

The first ambiguities, the ambiguity of which individual affects which, is addressed by the introduction of the definition of a connection (see Definition 3.3).

Definition 3.3 *Given that there is a symbiosis between two individuals A and B , a connection (denoted: $A \rightarrow B$, read: A affects B) exists if and only if the fitness of A has a direct affect on the fitness of B .*

Now the description of a symbiosis becomes more complete by simply listing all of the connections between a set of individuals. The second ambiguity in describing a connection is how, given $A \rightarrow B$, the fitness of A actually affects the fitness of B . Is the fitness of B wholly dependent on A or does the fitness of A produce only minor effects on the fitness of B ? This will be discussed at greater length in Section 4.2.1 and formal mathematical definitions will be proposed. However for the purpose of general classification two general types of connections need to be defined.

Definition 3.4 *The relationship $A \rightarrow B$ between individuals A and B is defined to be a protagonist connection $A \stackrel{+}{\rightarrow} B$ (read: A protagonizes B) if and only if there exists a connection $A \rightarrow B$ such that as the fitness of A increases, the fitness of B increases and as the fitness of A decreases the fitness of B decreases.*

Thus $A \stackrel{+}{\rightarrow} B$ implies that changes in the fitness of B mimic the changes in the fitness of A . Another general type of connection is the opposite of the protagonist connection.

Definition 3.5 *The relationship $A \rightarrow B$ between individuals A and B is defined to be an antagonist connection $A \stackrel{-}{\rightarrow} B$ (read: A antagonizes B) if and only if there exists a connection $A \rightarrow B$ such that as the fitness of A decreases, the fitness of B increases and as the fitness of A increases the fitness of B decreases.*

Thus $A \stackrel{-}{\rightarrow} B$ implies that changes in the fitness of B are opposite to the changes in the fitness of A . Using this notation it is possible to classify a variety of symbioses by the “structure” and types of connections in the symbioses.

3.2 Graphical Representation

After a short amount of experimentation it became clear that the connection notation was informative but became confusing when a large number of connections are involved. In order to simplify this information a graphical representation was developed. All of the connections representing the symbioses in the system are mapped into a Symbiosis Graph.

First, assume that there is a set of connections $\mathcal{C}$. For every individual in $\mathcal{C}$ a node is created in the Symbiosis Graph $\mathcal{G}$. Each node is then labeled according to the individual it represents (see Figure 3.1a). For every connection $A \rightarrow B$ in $\mathcal{C}$ a directed edge is created from node A to node B (see Figure 3.1b). All that remains is to label the directed edge with the appropriate connection type. If a connection is protagonist then it should be labeled using $+$. Alternately when a connection is antagonist it should be labeled using $-$ (see Figure 3.1c).

Figure 3.1: Construction of the graph for: $A \ominus B$, $B \oplus A$ and $A \oplus A$

This is not the first application of graphs to the study of ecological systems. Indeed there is a parallel of this work to the representation and simulation of food webs [31]. Food webs are the representation of the predator-prey relationships that exist in an ecosystem. For every predator-prey pair there is an edge in the graph (from the predator to the prey). The major difference between Food Webs and Symbiosis Graphs is what the nodes represent. In the Food Web assumptions are made about the prey of particular species and it is the predator-prey relationships between species that are graphed. In contrast, Symbiosis Graphs graph relationships between specific individuals. The reason that artificial relationships are commonly graphed in Symbiosis Graphs is the large complexity of a natural system. Even the smallest of naturally occurring closed systems would contain too many individuals and dynamic factors.

The motivation behind creating Symbiosis Graphs is the study of artificially generated ecosystems. It has always been the job of the ecologist and biologist to generalize, from observation, about the behaviour and interactions within an ecosystem. Using these long established generalizations, artificial systems can be generated and studied. The artificial systems can be created such that the Symbiosis Graphs have recurrent substructures. Thus the study of complex artificial systems becomes the study of common substructures and how multiple such structures interact.

Figure 3.2: Cyclic Symbiosis Graph

3.3 Feedback

One of the most interesting common features in Symbiosis Graphs is the presence of cycles. These cycles, or loops, in the graphs represent feedback in the fitness of the individuals. As defined by control theory, feedback is the portion of a system's output which modifies the input of the system. To clarify what is meant an example must be used. Consider the symbiosis between individuals A and B described by Figure 3.2. In this interaction A does not directly affect itself. However, consider the case where the fitness of A increases, because $A \stackrel{+}{\rightarrow} B$ the fitness of B increases. Since the fitness of B increases and because $B \stackrel{-}{\rightarrow} A$ the fitness of A decreases. Thus from the single increase in A there is a subsequent decrease in A . In this fashion A indirectly affects itself.

While cycles in the symbiosis graph may seem like a small detail, feedback has one of the biggest effects in natural or artificial ecosystems. Robertson and Grant noted that "feedback effects are of overriding importance in evolutionary theory not merely because they are ubiquitous but also because they generally dominate any process in which they are found" [57, p. 12]. The most formal study of feedback

effects has been in the area of control systems. In the design of control systems, feedback is the controlling element. By feeding the output of the system back into the input, allows the system to monitor itself and perform self corrections.

The behaviour of systems with feedback can be separated into two distinct forms. The first of these two forms is called unstable feedback. In an unstable feedback the process continually changes producing periodic or even chaotic fluctuations. In some cases the process is merely bounded and little else can be said. At other times the unstable feedback continually adds to itself, perpetually growing. Consider the phenomenon of uncontrolled population growth, also known as logistic growth. In logistic growth [69] the size of the population grows exponentially (this word is usually attributed to Malthus). A population begins at a certain size and grows. Each new member of the population can in turn reproduce and the process never ends.

In evolutionary theory such behaviour is often connected with the Red Queen Hypothesis proposed by Van Valen [67]. The Red Queen Hypothesis asks the question "Can a natural evolutionary system support continual change?". Also associated with continual change in a evolutionary system is the Rat Race (or evolutionary arms race) proposed by Rosenzweig [58]. In an arms race, the advance of a new offensive characteristic in a predator is met with an advance of a new defensive characteristic in its prey. Then the predator must develop a new offensive characteristic to defeat the prey's new defense. This phenomenon seems to continue forever with continual improvements on both sides. While the Red Queen Hypothesis is still questioned and debated [26], the realization of continual change in an artificial evolutionary system seems immanent³.

Feedback does not always have such a wild effect on systems. In fact the second and more frequent form, stable feedback, often represents a controlling influence. To demonstrate this control, two populations of individuals are needed, both capable of exponential population growth. If one population is the predator (e.g. fox) and the

³Work by Lindgren and Kauffman suggests this may have been realized. But no proof has been given that an artificial system can chaotically fluctuate indefinitely.

second is prey (e.g. hare), then there is a feedback created. When a population of foxes gets larger there are more hares killed and the population of hares gets smaller. This means that some foxes will starve and the number of foxes will decrease. In turn the hares are not killed as often and their population grows. The increase in the hare population leads to more food for the foxes, and the feedback loop is driven again. In this case neither population grows uncontrolled because of the effect of the other population. Thus the feedback cycle has “controlled” the populations’ sizes. The idea of stable feedback, that a system can be stable because its feedback balances its outputs, is the idea behind Evolutionary Stable Strategies (ESS). ESS is a key concept in an evolutionary modeling system originally proposed by John Maynard Smith and George Price [41] (See Section 4.1.2 for more details). As described by Maynard Smith, “an ESS is a phenotype such that, if all members of a population adopt it, then no mutant phenotype could invade the population under the influence of natural selection” [40, p. 10]. It was Maynard Smith’s idea that an evolutionary system would continue to introduce new phenotypes into a population until a stable population was found. Once the stable population existed any new phenotype introduced into the population would be inferior and natural selection would remove it.

This brief overview of feedback shows that the variety of behaviour created by stable and unstable feedback is exhibited in evolutionary systems. By recognizing the cycles in a symbiosis graph it may be possible to categorize the behaviour of the system. It only remains to further classify the types of feedback according to the specific types of connections involved in a cycle.

3.4 Types of Co-evolution

Before a classification of specific classes of co-evolution there are several issues to be addressed regarding symbiosis and co-evolution. Co-evolution as defined in Definition 3.2 is the result of natural selection and symbiosis. Unlike symbioses, which deal with the interrelationships of individuals, co-evolution marks which populations are

interrelated in their evolution. Thus it is possible to speak of the co-evolution of dogs and ticks. One further point should be made with regard to co-evolution. A population can co-evolve with itself. This may seem ludicrous but it is a consequence of the definition. A population that is evolving and contains symbioses only between individuals in its own population will evolve differently than a population that contains no symbioses. If a particularly unfit individual is in symbiosis with a better individual then it may survive to reproduce because of the symbiosis. This survival would not occur in the system without symbioses. Since different individuals survive then evolution with symbiosis within a population is different. Repeating this argument about populations with symbioses between them and populations without symbiosis leads to the same inferences and conclusion. Since the evolution of the system with symbioses between two populations is definitely co-evolution and the system with symbioses within a population is similar then they are both co-evolutionary.

While co-evolution occurs because of symbioses there are fundamental differences between them. Most importantly co-evolution deals with the interrelation of populations. symbioses are clearly defined to exist between individuals. Also co-evolution can be considered to constantly occur between two populations while symbiosis graphs do not remain constant for large periods of time. Suppose a tick were to begin its life on a dog named Fido and then half way through life move to a dog named Rex. Then the symbiosis graph would have to change the association between Fido and the tick to be between Rex and the tick. Worse yet, suppose there were five (5) ticks on Fido and Fido died. These five (5) ticks might find other dogs or (heaven forbid) a cat to live on. In this manner symbiosis graphs should be viewed as a varying entity.

The claim still remains that the classes of co-evolution are defined by specific recurrent substructures in symbiosis graphs. Take for an example the symbiosis graph in Figure 3.3 between five (5) ticks and the two (2) dogs that they live on. In the mean time it is important to notice that between dogs and ticks the connections are always the same. While the fitness of the individuals involved may differ and the exact effects of the connections will be different, the type of relationship between a

Figure 3.3: Symbiosis Graph for two Dogs and five Ticks

dog and a tick is always the same. Using a generalization of this type of relationship means that it is possible to say that predation (see Section 3.4.5) is the type of co-evolution that exists between dogs and ticks.

It is easily predictable that the symbiosis between any tick and any dog is of the same form. Ticks must perform certain tasks in order to survive. Due to their body structure, chemistry and intellect ticks can only have a limited type of interaction with a dog. This is true of all animals. Sustenance requirements, body structure, chemistry, sense capability, intellect and habitat all limit the forms of interaction possible between two species. For example a blue whale and a mountain goat are not likely to ever be in symbiosis. These limits have been known for years in ecological literature. Classification by field ecologists of symbioses has yielded a comprehensive set of definitions.

Field ecologists argue amongst themselves and with theoretical ecologists about what interactions exist and do not exist [66]. They also debate the classification scheme, what it should include or not include, how the general categories should be named [62].

The classification of types of co-evolution presented in the following chapters was prepared for this thesis. It represents a set of categories taken from previous works [64, 33] and redefined in terms of the definitions of symbiosis and connection (see Definitions 3.1 and 3.3). Not all ecologists or evolutionary ecologists will agree on the definitions presented. However the definitions were necessary to aid in classification

of co-evolution and the creation of these definitions was done in such a way as to be consistent and clear. In every possible instance the categories described below were held consistent to the works of Starr [64] and Lewis [33].

Since each specific type of symbiosis can cause a type of co-evolution then it is appropriate to name all types of co-evolution to be identical to the name of the symbiosis that causes it. Thus each of the following sections refers to a form of symbiosis and the type of co-evolution that it causes.

3.4.1 Commensalism

Commensalism is one of the two forms of co-evolution that does not involve direct feedback in the symbiosis graph. In commensalism the symbiosis is between two individuals, the host and the commensal. Informally the commensal is said to derive benefit from the host without affecting the host. An excellent example of commensalism is between the shark and the remora fish [8]. The remora fish is a small fish that developed a suction cup into its dorsal (or bottom) fin. The remora fish uses this suction cup to attach itself to the shark so as to travel with the shark. When the shark feeds, it is often a messy experience with bits of its prey floating in the water. By traveling with the shark, the remora fish is able to eat these remnants without expense to the shark. Thus the remora is benefiting from the shark without affecting the shark⁴. This definition of commensalism does not explain how the symbiosis translates into effects on the fitness of the host and commensal.

Since the host is unaffected by the commensal, then the host's fitness does not change directly as a result of a change in fitness in the commensal (and hence no feedback). However the commensal derives benefit from the host, so a change in the host's fitness would affect the commensal. If the host's fitness were to increase then it could be inferred that the commensal could derive greater benefit from the host, thereby increasing the commensal's fitness. If the host's fitness were to decrease then

⁴Arguments could be made that the remora fish causes more drag to the shark or that the remora fish is stealing food from the shark; but, these effects are deemed frivolous.

Figure 3.4: Symbiosis Graph for Commensalism

by the same reasoning the commensal might derive less benefit, thereby decreasing the fitness of the commensal.

Examining the effects on the fitness of the commensal shows that the host's connection to the commensal is a direct or indirect protagonist connection (see Definitions 3.4 and 3.12). This means that in a symbiosis graph the commensal and the host would look like Figure 3.4 and would be defined by Definition 3.6.

Definition 3.6 *Commensalism occurs between two individuals $Host$ and $Commensal$ if and only if $Host \stackrel{+}{\rightarrow} Commensal$ such that $Commensal$ does not affect the fitness of $Host$.*

3.4.2 Amensalism

Amensalism is the second form of co-evolution that does not involve feedback in its symbiosis. In amensalism the symbiosis is between two individuals, the host and the amensal. Informally the amensal is detrimentally affected by the host and the host is unaffected by the amensal. Amensalism is also the least mentioned of all the types of symbiosis. Named by Lewis in [33] Amensalism is almost never mentioned in the classification of animal relationships. This is, most likely, due to the fact

that it seems an unnatural association. Typically an individual only produces a detrimental affect on someone for a reason. Revenge for a previous detrimental effect or to derive benefit would normally be reasons to produce a detrimental effect and these relationships are not amensalism.

Ironically, an example of amensalism has already been presented in this work: the example of the beaver affecting the fish by building a dam. By building a dam, the beaver produces a large detrimental effect on the fish's environment. However the fish does not affect the beaver at all. Thus the beaver is the host and the fish is the amensal.

To describe this concept more accurately an analysis of how fitness changes in the beaver produce fitness changes in the fish is necessary. Given that the fitness of the beaver increases then it will be able to produce a better dam and the fish will have even less of a river to swim in and the fish's fitness will decrease. If the fitness of the beaver were to decrease then it will not be able to produce as good a dam. This means there may be more of a river for the fish to swim in and the fish's fitness will increase.

Comparing this type of connection to those previously defined shows that the beaver of this example antagonizes the fish ($beaver \dashv fish$). Thus the formal definition of amensalism is given in Definition 3.7 and is represented in a symbiosis graph as shown in 3.5.

Definition 3.7 *Amensalism occurs between two individuals Host and Amensal if and only if $Host \dashv Amensal$ such that Amensal does not affect the fitness of Host.*

3.4.3 Mutualism

Mutualism is the first form of co-evolution, dealt with here, that contains feedback in its symbiosis. Informally mutualism is a relationship between two individuals, called symbionts⁵, where both symbionts derive benefit from the other. While every-

⁵In symbioses here one symbiont contains the other or is much larger the term host is used. This form of usage is quite common. Only Symbiont is used here to avoid confusion with the use of host elsewhere.

Figure 3.5: Symbiosis Graph for Amensalism

one would concur with this definition of mutualism. the exact description of what mutualistic symbiosis is not agreed upon[33, 38]. The variety of controversial forms of mutualistic symbiosis are those that are temporary (recurrent or not). For Margulis [38] the definition of mutualistic symbiosis does not include these non-persistent forms. According to her, any form of symbiosis requires “physical contact between organisms ... throughout a significant portion of the events in the development of an individual organism ...”[38, p. 2]. This means that a relationship that is temporary such as pollination of flowers by bees does not qualify as a form of symbiosis[62]. This is despite the fact that the bee is receiving sustenance and the flower gets to spread its pollen. In deference to this idea Lewis and Starr [33, 64] recognize the temporary and persistent forms of symbiosis and it is this definition that is adopted here.

To accurately discuss the behaviour of all types of mutualism would take volumes. Variations of dependence, spatial, temporal and genetic relationships are enormous and interesting. However the example of microflora in vertebrate guts seems a good example⁶ to describe typical mutualistic behaviour. Within four different orders of mammalia alone evolution has separately led to the mutualism between the mam-

⁶The following is adapted from [62, chap. 8].

mals and bacteria that inhabit their foreguts. Of these orders the family of ruminants (which includes cows and sheep) contain bacteria which are capable of digesting the polysaccharides that dominate the ruminants diet.

Suppose a cow's fitness increases then it will be able to eat more or produce offspring. This means that there will be more food for the bacteria or a new individual (the calf) to produce bacterial offspring for. Thus the bacteria will increase in fitness. However should the cow's fitness decrease then the bacteria will have a worse environment (e.g. a different temperature in the cow's foregut) and/or less food to digest. Thus the bacteria will decrease in fitness.

By a similar analysis, suppose the fitness of the bacteria were to decrease⁷. Then the cow would not attain as much of the sugar normally produced by the bacteria and the cow's fitness would suffer. Given that the bacteria increased in fitness then the cow could receive more vitamins and sugars from the digesting material. Thus the cow's fitness would increase.

Careful examination shows that there are two connections and that the cow and bacteria protagonize each other ($Cow \pm Bacteria$ and $Bacteria \pm Cow$). This can be generalized to the definition of mutualism given in Definition 3.8. The typical mutualism is displayed in a symbiosis graph as shown in Figure 3.6

Definition 3.8 *Mutualism occurs between two individuals SymbiontA and SymbiontB if and only if $SymbiontA \pm SymbiontB$ and $SymbiontB \pm SymbiontA$.*

3.4.4 Competition

Competition is yet another form of co-evolution that has feedback within its symbiosis. Most people are familiar with the term 'competition'. The idea is that there is a limited resource critical to fitness that two individuals (called competitors) both must have. They compete for the limited resource and one takes the resource (or

⁷Assume for the sake of the example that the bacteria's fitness changes as a group. The actuality is that the bacteria are in a complex interaction of competitions that are not easily modeled

Figure 3.6: Symbiosis Graph for Mutualism

the majority of the resource). Common factors that individuals compete for, are hunting territory, mating rights and food resources.

It is possible to use the bacteria from the previous section as an example of competition. Within a cow, the different species of bacteria that perform digestion can number as many as 200 with as many as 50 species of protozoa aiding in the digestion process. It is also recognized that the protozoa perform the same digestion task as some of the bacteria [62]. To study the example, consider that the bacteria and the protozoa each behaving as a separate group with each group's fitness fluctuating as a whole.

If the protozoa's fitness decreases then they cannot digest as much food and the bacteria have more food to digest. This leads to an increase in the fitness of the bacteria. However, when the protozoa's fitness increases they are able to digest more and the bacteria will have less food to digest. As a result the bacteria's fitness decreases.

Due to the symmetry of the relationship the bacteria has the same effects on the protozoa that the protozoa has on the bacteria. Thus by Definition 3.5 the protozoa antagonizes the bacteria and vice-versa (i.e. $Protozoa \rhd Bacteria$ and

Figure 3.7: Symbiosis Graph for Competition

Bacteria $\rightleftharpoons$ *Protozoa*). Generalizing the relationship to any competition gives Definition 3.9 which is displayed in a symbiosis graph in Figure 3.9.

Definition 3.9 *Competition occurs between two individuals Competitor A and Competitor B if and only if Competitor A $\rightleftharpoons$ Competitor B and Competitor B $\rightleftharpoons$ Competitor A.*

3.4.5 Predation

Predation, like the others discussed here, encompasses a sweeping range of inter-population relationships. Named Agonism by Lewis [33]⁸ this form of co-evolution also encompasses feedback within the symbiosis that causes the co-evolution. The word predation, comes from the root predator, and indicates the presence of a predator and its prey. Informally predation is between two individuals, the predator that derives benefit from the prey, and the prey that is detrimentally affected by the predator.

As the names indicate the predator-prey relationship is one type of relationship that causes the predation form of co-evolution. The other common relationship

⁸The term Predation is more popular in all other literature and will be used here.

causing predation is the parasite-host relationship (the parasite taking the role of predator and the host taking the role of the prey). Re-examining the example of the fox and hare shows the nature of predation.

Suppose the fox's fitness increases, then it will be able to hunt the hare more often (or better). This means that the hare's fitness will decrease. In contrast suppose that the fox's fitness decreases then the hare will not be chased as long (or as often). As a result the hare's fitness will increase.

Also, suppose that the hare's fitness increases, it will be able to out run the fox with higher probability. This implies that the fox's expected fitness will decrease. If the hare's fitness decreases then fox will be able to catch the hare with higher probability. Therefore the fox's expected fitness will increase.⁹

Examining the types of connections described shows that the fox antagonizes the hare and the hare protagonizes the fox ($For \bar{=} Hare$ and $Hare \bar{=} For$). Generalizing this form of symbiosis yields Definition 3.10 which is shown in Figure 3.8.

Definition 3.10 *Predation occurs between two individuals Predator and Prey if and only if $Predator \bar{=} Prey$ and $Prey \bar{=} Predator$.*

3.4.6 Adaptism

This chapter has, up until this point, dealt with the case of an individual's fitness being affected by another individual. The different cases presented showed that these symbioses lead to the different forms of co-evolution. However this leaves two cases that are not included within the previous categories: i) the individuals that modify their environment producing an affect on their own fitness and ii) the individuals that modify themselves producing an affect on their own fitness. This modification to the individual must be done without the aid of another individual

⁹The wording of this analysis is important. Proper analysis of this type of system requires probability because to say that a dead hare has less fitness seem ridiculous. Describing the average case and what is expected to happen describes the behaviour in a more meaningful manner.

Figure 3.8: Symbiosis Graph for Predation

or it is obviously co-evolution of another sort. For clarity these individuals will be referred to as adaptive individuals.

Typically adaptive individuals are ignored in ecology literature because they represent most naturally occurring individuals. However, from a theoretical point of view these two adaptations should be considered very seriously. In mutualism two beavers might build and maintain a dam and benefit from that dam. In modeling the fitness of the beavers the dam is very important and represents a symbiosis between the beavers. But suppose that the same beaver simply builds a dam by itself. The beaver will definitely benefit in the future from having built the dam. In this manner the beaver has a fitness connection to itself.

Informally the definition of Adaptism is when an individual, without assistance from another individual, adapts its surroundings or itself and affects its own fitness. Suppose that an adaptive individual's fitness increases. Presumably the adaptive individual's fitness will increase later as a result of this initial increase. Likewise should the adaptive individual's fitness decrease it may then decrease further as a result (Weaknesses or strengths in the immune system of an individual may lead to greater strengths or weaknesses respectively). Because of the wide range of possibilities for adaptive individuals the definition of Adaptism (see Definition 3.11)

Figure 3.9: Symbiosis Graph for Adaptism

is necessarily general. It should also be noted that either of the graphs shown in Figure 3.9 can be considered to lead to Adaptism¹⁰.

Definition 3.11 *Given one individual, Adaptism occurs if and only if Individual $\stackrel{+}{\rightarrow}$ Individual or Individual $\stackrel{-}{\rightarrow}$ Individual.*

3.4.7 Indirect and Ambiguous Types of Co-evolution

In the original definition of co-evolution (see Definition 3.2) it is very clear that two populations only co-evolve when there is a symbiosis between the populations. Since symbiosis only exists between individuals where one individual has a direct effect upon the other's fitness then this does not account for co-evolution because of indirect effects on an individual. While this may seem too restrictive it allowed for a clear and precise definition of co-evolution and the forms of co-evolution. It is the purpose of this section to introduce some of the problems associated with indirect effects, and propose a limited method of analysis to deal with the clear cases of indirect effects.

To begin with, an analog of protagonist and antagonist connections will be needed that are based on indirect affects only. Using this concept the indirect protagonist and antagonist connections are given by Definitions 3.12 and 3.13. The

¹⁰The author cannot provide an example of a creature antagonizing itself but it is provided as a form of adaptism to make the model complete.

Figure 3.10: $A \oplus B$ and $A \ominus B$

subsequent additions to symbiosis graph notation will also be made such that labeling remains constant with previous labeling of edges and the edges of an indirect nature will be drawn with a dashed arrow (See Figure 3.10 for examples)

Definition 3.12 An indirect protagonist connection $A \oplus B$ (read: *A indirectly protagonizes B*) is said to exist between individuals *A* and *B* if and only if the fitness of *A* indirectly affects the fitness of *B* and when the fitness of *A* increases the fitness of *B* increases and when the fitness of *A* decreases the fitness of *B* decreases.

Definition 3.13 An indirect antagonist connection $A \ominus B$ (read: *A indirectly antagonizes B*) is said to exist between individuals *A* and *B* if and only if the fitness of *A* indirectly affects the fitness of *B* and when the fitness of *A* increases the fitness of *B* decreases and when the fitness of *A* decreases the fitness of *B* increases.

Given the two definitions of indirect connections it should now be possible to infer from direct connections some indirect connections. Using three individuals *A*, *B*, and *C*, consider the four following cases:

1. $A \pm B \pm C$

For this case, when the fitness of *A* increases, *B* also increases and *C* increases. Likewise when the fitness of *A* decreases, *B* also decreases and *C* decreases. Thus $A \oplus C$ follows from Case 1.

Figure 3.11: Constructing Indirect Connections

2. $A \bar{=} B \bar{=} C$

For this case, when the fitness of A increases, B decreases and C increases. Likewise when the fitness of A decreases, B increases and C decreases. Thus $A \hat{=} C$ follows from Case 2.

3. $A \pm B \bar{=} C$

For this case, when the fitness of A increases, B also increases and C decreases. Likewise when the fitness of A decreases, B also decreases and C increases. Thus $A \hat{=} C$ follows from Case 3.

4. $A \bar{=} B \pm C$

For this case, when the fitness of A increases, B decreases and C decreases. Likewise when the fitness of A decreases, B increases and C increases. Thus $A \hat{=} C$ follows from Case 4.

Since indirect connections are analogous to their direct counterparts it is easy to summarize the rules of obtaining indirect connections from direct and indirect connections (see Table 3.4.7). For a specific example of a symbiosis graph before and after the addition of indirect connections see Figure 3.11.

While the use of indirect connections may clarify the relationship between two indirectly connected individuals there are ambiguous cases where confusion results from the drawing of indirect connections. One of the easiest to illustrate is the case

Case	$A \multimap B$	$B \multimap C$	$A \multimap C$
1	$A \vdash B$	$B \vdash C$	$A \hat{=} C$
	or	or	
	$A \hat{=} B$	$B \hat{=} C$	
2	$A \multimap B$	$B \multimap C$	$A \hat{=} C$
	or	or	
	$A \hat{=} B$	$B \hat{=} C$	
3	$A \vdash B$	$B \multimap C$	$A \hat{=} C$
	or	or	
	$A \hat{=} B$	$B \hat{=} C$	
4	$A \multimap B$	$B \vdash C$	$A \hat{=} C$
	or	or	
	$A \hat{=} B$	$B \hat{=} C$	

Table 3.1: Summary of Indirect Connection Rules

Figure 3.12: A Simple Ambiguous Symbiosis Graph

shown in Figure 3.12. In this figure it is obvious that *A* antagonizes *C* while *A* indirectly protagonizes *C*. Only through a mathematical simulation of the system could the true relationship of *A* and *C* be observed. This merely emphasizes that the system of classification presented here is as clear as was possible given the generality of the systems dealt with. Clear understanding of relationships requires a formal modeling system and a simulation of that system.

Chapter 4

Computer Modeling of Co-evolution

In discussing the modeling of co-evolution it is important to state the definition of co-evolution used. This is important because the generality of the definition used will indicate what models deal with co-evolution. Co-evolution as discussed here was previously defined in Definition 3.2. By this definition, a minimal condition for co-evolution to exist, is that the fitness function of one individual must be mathematically dependent on the fitness function of another individual.

Before listing and describing the models of co-evolution it is necessary to describe what is meant by a model and how such models might be implemented. Informally, a model is a mathematical, graphical or conceptual representation of a system or knowledge about a system. Since the definition of a model is not the topic of interest, this informal definition shall be the only one given. If further clarification is required examples of models are given in Section 4.1.

Of interest to this thesis is the question “What types of models exist?”. Keddy gives a good introduction to the topic in [29, p. 48-50] while discussing the details of a model classification scheme of his own. This scheme will be used in this chapter to aid in the description of previous work.

Keddy’s scheme breaks models into three categories: Predictives, Exploratory and Descriptive. These categories are not mutually exclusive although it is rare to define a model that belongs to all three categories.

4.1 Related Work

Models of co-evolution have several distinguishing characteristics. Just modeling the populations involved in an instance of co-evolution is difficult. A population can be modeled as a single entity with several distinguishing traits (e.g. size, fitness,...), it can be modeled as a distribution of fitnesses or it could be thought of as a list of individuals each with their own fitness. This does not even mention the idea of spatial relationships, inter-dependencies, symbioses or mating between individuals.

One of the most important choices to be made, while modeling co-evolution, is the decision whether or not to use a predictive model or an exploratory model. In order to make a predictive model the independent and dependent variables must be measurable. Since the fitness of an individual is not measurable (see Section 1.2) it is impossible to predict what the fitness of an individual is. Due to this, the predictive models involving co-evolution often predict the size of the population. To give a comprehensive overview of the various choices when modeling co-evolution is beyond the scope of this work. However it is important to discuss the variety of models from previous work. Also presented in this section are models that are not co-evolutionary but are related to models that are.

4.1.1 Population Growth Models

There are a number of models that try to predict the population size of one or more populations. Of these models many involve the co-evolution of one or more species. It seems only natural to include the more basic of these models, even though they are not co-evolutionary in nature. The following is a summary of the more detailed analyses on population growth models in [29, 69, 22, 18].

The simplest, non-co-evolutionary population growth model is the Exponential Growth Equation attributed to Malthus[37]. In this model, represented by Equation 4.1, the intrinsic growth rate of the population $\frac{N'(t)}{N(t)}$ (i.e., the growth per individual in the population) is a constant r . In an unconstrained system it is assumed that

each member of the population will reproduce at a constant rate¹.

$$\begin{aligned}\frac{N'(t)}{N(t)} &= \frac{\frac{dN(t)}{dt}}{N(t)} = r \\ \Rightarrow N(t) &= N(0) \exp^{rt}\end{aligned}\tag{4.1}$$

If this model seems overly simplified it is because it is overly simplified. There is no concept of age distribution amongst the population. There is no accounting for the varying reproductive abilities of individuals as they age. These arguments imply that as a descriptive model the Exponential Growth Equation is very poor. The erroneous assumption is that if the net birth rate remains the same then this model should accurately predict the population growth of a species. This is a bad assumption because no real environment can support an ever increasing population. Eventually the population will run out of a fixed resource (e.g. food, space, air,...). This implies that in reality there is a maximum supportable population whereas $N(t) = N(0) \exp^{rt}$ has no upper bound.

The second model, which was not described as co-evolutionary by its authors, is the Logistic Growth Equation. The Logistic Growth Equation was originally explained by Lotka [36] but is attributed to Verhulst. This model, represented by Equation 4.2, represents a single population in a constrained environment. Using the same notation as the Exponential Growth Equation, the Logistic Growth Equation introduces the carrying capacity K . The carrying capacity is the maximum size of the population that can be supported by its environment. For a more detailed history of Malthus, Verhulst and early thoughts on population growth the reader should consult Hutchinson[22].

$$\frac{dN}{dt} = rN \frac{K - N}{K}\tag{4.2}$$

¹As with all population growth models presented here there is the assumption that children are born from at least one parent (no spontaneous generation) and that the population size is a real value. This allows continuous calculus to be applied.

As an exploratory model Equation 4.2 is very good. While it is not perfect, it does mimic the constrained growth of many species. However as a predictive model it often fails. A classic failure quoted by Waltman[69] was that Pearl, Reed and Kisch [50] predicted the US population to be 15-20% lower than what was attained in 1970. In trying to remove some of the predictive error several variations of the Logistic Growth Equation have been formulated. Hutchinson [22] enumerates and describes many of them.

The Lotka-Volterra Model is another exploratory model that predicts the population sizes of S populations in theoretical co-evolutionary settings. This model was independently proposed as an exploratory model of competitive population dynamics by Lotka[36] and Volterra[68]. More recently it has been modified to include the co-evolutionary models of mutualism, predation and competition[39, 52, 59].

The model itself is a set of S equations that relate the type and strength of interactions between populations. Conceptually, the equations are extensions of the Logistic Growth Equation (4.2)². Every population i 's size, $N_i(t)$, changes as a function of time. The equation for the rate of change of the population size at a time t , $\frac{dN_i(t)}{dt}$, is given by Equation 4.3.

$$\frac{dN_i(t)}{dt} = N_i(t) \left(r_i + \sum_{j=1}^S a_{ij} N_j(t) \right) \quad (4.3)$$

The meanings of r_i and a_{ij} are of great interest to this thesis. In a real system these may vary, however in these equations they are considered "constants". As with the previous two models the constant r_i represents the net birth rate. However, the meaning of a_{ij} seems unclear. Suppose, $a_{ij} = a_{ji} = 0$, then the two populations do not have a direct interaction.

To analyze the forms of co-evolution, suppose that a connection is between populations instead of individuals. Further suppose that instead of populations affecting each others' fitnesses they affected each others' population size. After making these suppositions it is possible to ascribe meanings to the cases i) $a_{ik} > 0$ and ii) $a_{ik} < 0$.

²The following is adapted from Pimm [52]. Notation is changed to reflect that of the previous paragraphs.

Form of Co-evolution	Conditions Necessary	Populations' Role
Commensalism	$a_{ik} > 0$ $a_{ki} = 0$	k is the host i is the commensal
Amensalism	$a_{ik} < 0$ $a_{ki} = 0$	k is the host i is the amensal
Mutualism	$a_{ik} > 0$ $a_{ki} > 0$	k is a symbiont i is a symbiont
Competition	$a_{ik} < 0$ $a_{ki} < 0$	k is the competitor i is the competitor
Predation	$a_{ik} > 0$ $a_{ki} < 0$	k is the prey i is the predator

Table 4.1: Forms of Co-evolution within the Lotka-Volterra Model

For $a_{ik} > 0$, k protagonizes i ($k \stackrel{+}{\sim} i$) and for $a_{ik} < 0$, k antagonizes i ($k \stackrel{-}{\sim} i$)(See Section A.1 for details).

Having established that the sign of a_{ij} corresponds to the type of “connection”³ between populations. Since the forms of evolution are defined in terms of these connections (see Sections 3.4.1 to 3.4.6) the Table 4.1.1 can be compiled with the conditions necessary to form the various types of co-evolution within the Lotka-Volterra model⁴.

Given this interpretation of the Lotka-Volterra model, it is important to re-examine the Logistic Growth Equation. The interpretation of the term $\frac{r}{K}N^2$ is that the population antagonizes itself. This makes sense because the term was originally added to account for competition within the species. Using the definition of co-

³Remember that a connection is between individuals, its definition was only extended for the purpose of analysis.

⁴The end result of this analysis is an expanded version of Pimm’s [52]; however, the technique used conforms to the definitions provided in Chapter 3.

evolution found here the Logistic Growth Equation (4.2) represents a population in co-evolution with itself.

This model of co-evolution is one of the nicest because of its ability to clearly define the strength and type of relationship between populations independent of each other. It is then possible to study the effect of multiple relationships occurring at once.

4.1.2 Evolutionary Game Theory and Stable Strategies

In 1973 John Maynard Smith and George Price [41] introduced the concepts of Evolutionary Game Theory and Evolutionary Stable Strategies (ESS) that would develop into one of the largest areas of co-evolution research. In his later book Maynard Smith generalized the definition of an ESS to be “a phenotype such that, if all members of a population adopt it, then no mutant phenotype could invade the population under the influence of natural selection” [40, p. 10].

The general idea of ESS is that an evolutionary system can fall into a specific configuration and no new individuals introduced into the system will move it away from that configuration.

Of specific interest, to this work, is the topic of the original paper by Maynard Smith and Price. It was the first paper to apply Game Theory to evolutionary problems[12]. The topic of the paper [41] was conflict between animals. In his model Maynard Smith used Price’s idea [12] of modeling the interaction between individuals as a game. Once that was done, an analysis of the population(s) could be performed using Game Theory. Using this Evolutionary Game Theory model it is possible to explore a wide range of co-evolutionary possibilities.

Within Evolutionary Game Theory (EGT) every specific model has its own assumptions. A comprehensive survey of specific models within EGT is beyond the scope of this work. However, it is enlightening to describe a specific model and list its assumptions. For this purpose the Hawk-Dove example, provided below, is one adapted from Maynard Smith’s book [40].

As with most models in EGT it is assumed that interaction between individuals can be categorized by a two person game. In introducing the Hawk-Dove model of competition the following assumptions are made:

- There is one infinite sized population containing all individuals
- Reproduction is asexual
- Individuals with higher fitness reproduce more often
- Contests occur between two individuals and
- An individual has constant behaviour throughout its existence

The Hawk-Dove model is a model of competition between two individuals for a resource. In this model it is assumed that an individual displays either Hawk behaviour or Dove behaviour. When an individual displays Hawk behaviour it always attacks its opponent. A Hawk does not stop attacking until it is injured or it has obtained all of the resource. A Dove, on the other hand only threatens to attack its opponent. If the Dove is not attacked it shares the resource; but if the Dove is attacked then it gives up all of the resource.

Case i) Dove vs. Dove Since both Doves will only threaten to attack they will share the resource. If the value of the average resource is V then in the average Dove vs. Dove competition each Dove will receive $\frac{V}{2}$. Using statistical notation the expected return of a Dove vs. Dove conflict is $\frac{V}{2}$ (i.e., $E(D, D) = \frac{V}{2}$).

Case ii) Hawk vs. Hawk Since both Hawks attack, one Hawk will be rewarded and the other will be injured. It is assumed that all hawks are equal, this implies that there is a 50% chance of the Hawk being injured and a 50% chance of it gaining the resource. Associating an average cost C with being injured will result in an expected return of $E(D, D) = \frac{1}{2}(V - C)$.

Case iii) Dove vs. Hawk Since the Hawk attacks and the Dove will run away then the Hawk can expect all of the average resource during a Hawk vs. Dove competition (i.e., the Hawk receives $E(H, D) = V$). In contrast the Dove can expect to get no resource during the Dove vs. Hawk competition (i.e., $E(D, H) = 0$).

Suppose that the population is made up entirely of Doves. Hawks could invade the population and thrive because whenever they meet with a Dove they would get all of the resource. In this way a population of all doves is not an ESS. If the population is made up of a combination of Hawks and Doves the situation is not as clear. Using previous analysis of this system there is only one ESS of the system (See Section A.2 or [40, p. 11-17] for details). This ESS is equivalent to $p = \min(1, \frac{V}{C})$

This particular model of competition between two types of individuals, has been fully explored. The typical format for EGT models begins with the establishment of behaviour types, expected returns and the probabilities of various outcomes are determined. In this case it is easy to see what happens but there can be cases where more than one ESS exists for a system or no ESS exists at all. In these cases behaviour of the system is much more dynamic and interesting.

There are just some final words of caution regarding EGT. There is no set of behaviours that accurately mimics a real population. This system is strictly for the exploration of relationships and theoretical co-evolution. Tying too much meaning into a specific model can result in inaccurate extrapolations about behaviour of real systems.

4.1.3 The NK Fitness Landscape and The NK Competition Model

The NK fitness landscape was created by Kauffman and Weinberger[28] as an exploratory model of single population fitness landscapes and was later extended to the NK competition model. An individual in the NK landscape has a “genotype” of N genes. In the landscape’s simplest implementation each gene has two possible

alleles (0 or 1). Thus an individual is expressed as a binary string of length N and the set of all possible individuals is of size 2^N . For every gene j , K other genes are specified that alter the fitness of gene j . Thus there is a different fitness contribution for all 2^{K+1} combinations of gene j and the alleles(0's or 1's) in its K associated genes. It is Kauffman's claim that only the sizes of N and K matter and that the distribution of K is far less important[26, p. 42].

For each landscape a 2^{K+1} by N matrix $\mathcal{V}$, is used for fitness contributions⁵. Every entry v_{ij} in $\mathcal{V}$ is created from a uniform random distribution between 0.0 and 1.0. Each v_{ij} represents the fitness contribution w_j by gene j for the i^{th} combination⁶ of gene j and its K associated genes. Given $\mathcal{V}$, the fitness of W an individual in the landscape can be calculated as the average of its contributions w_j .

Before creating this example with $N = 3$ and $K = 1$, it is always necessary to specify which genes affect which genes. It will be assumed that every gene j will be affected by its right neighbour(see Figure 4.1.3a). As previously defined, the matrix $\mathcal{V}$ is randomly generated. The matrix $\mathcal{V}$ for this example is given in Equation 4.4.

$$\begin{array}{c|ccc} \text{Gene} & 1 & 2 & 3 \\ \hline \text{Combination} & & & \\ \hline 00 & 0.8 & 0.3 & 0.4 \\ 01 & 0.8 & 0.1 & 0.2 \\ 10 & 0.2 & 0.6 & 0.5 \\ 11 & 0.9 & 0.7 & 0.1 \end{array} = \mathcal{V} \quad (4.4)$$

Suppose the individual to be evaluated was 110. Then, by the fitness calculation given in Table 4.2, the fitness of 110 is 0.66.

The most interesting gene contribution is the one made by gene 3. Since gene 3 is associated with gene 1 (see Figure 4.1.3a) the combination is 10. This is because the combination is taken in order, as displayed by the emphasis in Table 4.2. By

⁵Kauffman and Weinberger did not name this matrix; but it was necessarily introduced to avoid confusion. It is not necessary to create the entire matrix. The required portions of the matrix can be created dynamically with each problem instance and each entry stored in case the entry is required again.

⁶the i^{th} combination being i^{th} in a lexical ordering of the combinations.

Gene	Combination	Fitness Contribution
1	110 = 11	$w_1 = v_{41} = 0.9$
2	110 = 10	$w_2 = v_{32} = 0.6$
3	100 = 10	$w_3 = v_{33} = 0.5$
Fitness ($W = \frac{1}{N} \sum_{i=1}^N w_i$)		$\frac{0.9+0.6+0.5}{3} = 0.66$

Table 4.2: Calculation of Fitness of 110 in an NK model

Individual	w_1	w_2	w_3	W
000	0.8	0.3	0.4	0.500
001	0.8	0.1	0.2	0.566
010	0.8	0.6	0.4	0.600
011	0.8	0.7	0.2	0.566
100	0.2	0.3	0.5	0.333
101	0.2	0.1	0.1	0.133
110	0.9	0.6	0.5	0.666
111	0.9	0.7	0.1	0.566

Table 4.3: Fitnesses of all Individuals in an NK model

performing the same calculation, the fitnesses are as shown in Table 4.3 and in Figure 4.1.3b.

The NK fitness landscape deserves some comments. What Kauffman and Weinberger have created is a fitness landscape that is tunably rugged. What this means is that binary strings are single bit mutant neighbours (i.e., those connected on a hypercube mapping of binary strings) have either highly correlated or uncorrelated fitness. For example, when $K = 0$ the fitness of single bit mutants is highly correlated. So much so that by traveling from one individual x to a higher fitness, single

Figure 4.1: NK Fitness Example

bit mutation of x the global maximum can always be found. As K increases the neighbours become less and less correlated and multiple local optimum appear.

The example can be used to clarify the meaning of these statements. Looking at Figure 4.1.3b consider that individuals are single bit mutant neighbours if and only if they are joined by a line. In this particular example there are two local optima: 001 and 110 (each is circled). By the definition of local optimum these two individuals are one bit mutations of individuals of the same or lower fitness. In a $K = 0$ system there is only one local optimum, while in a system with $N = K - 1$ there are a large number of local optima[26]. This concept of tunable ruggedness (i.e., as K increases the number of local optima increases) is important to the analysis of NK Co-evolutionary (NKC) models.

A major part of Kauffman's⁷ analysis of his NKC model pertains to the concept of Nash Equilibria. Nash Equilibria are conceptually very similar to ESS. In fact Kauffman suggests that "[ESS is a refinement of Nash Equilibria]" [26, p. 245]. Nash Equilibrium can be described as a steady state in which mutations of any or all individuals in the NKC model will not produce a change in the system. Kauffman argues that because all of the individuals in a population mutate at once that this is different from the ESS's single mutant phenotype invasion.

The topics of Kauffman and Johnsen's research into NKC models can be broken down into two stages: exploration of the properties of co-evolutionary landscapes and exploration of the development of interactions between species. In order to perform both of these explorations two similar models were developed. The calculation of the fitness of an individual throughout both stages of NKC research was done on what Kauffman and Johnsen called the NKC fitness landscape. This is an extension of the NK fitness presented above.

In the NKC model as in the NK model the fitness of an individual is the average of each gene's contribution. The given gene j is dependent on the alleles in K other

⁷Kauffman is usually attributed to the analysis and experimentation of the NKC model. His association with co-authors has been sporadic. Wherever possible other contributors have been cited.

genes within the same individual and on C other genes in S different individuals. Kauffman and Johnsen assumed that a fitness dependency is a symmetric relationship. This means that if individual x depends on individual y for C genes, then the reverse is also true. Given this dependency two individuals are described as being in each other's niche. To contain all of the different possible fitness contributions, the matrix $\mathcal{V}$ is expanded to be 2^{K+SC+1} by N . Besides this there are no differences between the NKC fitness calculation and the NK fitness calculation.

Both models deal specifically with the fitness of individuals, each represented by binary strings, in S different populations. All populations (Kauffman occasionally refers to them as species) are assumed to be homogeneous (i.e., each population consists of identical individuals). Thus the fitness of a population is the fitness of one individual in that population. A population is assumed to "evolve" by a process of single bit mutations. With every "generation" a population (representable by a single individual) has one of its bits changed at random from 1 to 0 or vice-versa. The fitness of the new mutation is then calculated. The original individual is replaced by the new individual if and only if the fitness of the new individual is strictly higher than the fitness of the original individual. In subsequent generations a different population is mutated and this process is continued until all the populations have been cycled and then the process starts again.

In the first model, species are interconnected but population size is not considered. Kauffman examines variations of N, K and C across different size groups of S . Kauffman obtains clear and definable characteristics from this model. His research stands as a thorough examination of a fitness landscape and co-evolutionary model. Specifically he looks at the length of time to achieve a Nash Equilibrium, average fitness of populations and how varying the N, K and C parameters affects these quantities. He also examined populations that were spatially located on a grid. Each population was connected to its horizontal and vertical neighbours. Kauffman then plotted the parts of the system that were changing. Each of his analyses and summaries is interesting and informative[26].

In the second model, each population is given a population size which are related

by the Lotka-Volterra population growth equations. Kauffman and Johnsen [27] define the constants of the Lotka-Volterra Equations to be related to the fitnesses of the populations. Two components of a gene's fitness are defined, $f_{iso}(i)$ which is the fitness of individual i when it was isolated from the other populations and $f_{conn}(i, j)$ ⁸ which is the additional fitness for species i given that it interacts with species j . It is also assumed that there is a single carrying capacity $\mathcal{K}$ for all populations. With these quantities defined, the constants of the Lotka-Volterra model are given by Equations 4.6.

$$\begin{aligned} r_i &= f_{iso}(i) - 0.5 \\ a_{ii} &= -\frac{1}{\mathcal{K}} \end{aligned} \tag{4.5}$$

$$a_{ij} = \frac{1}{\mathcal{K}}(f_{conn}(i, j) - 0.5) \tag{4.6}$$

In both models it was discovered that when an individual's K values are high the landscape of each individual is riddled with local optima. This results in a higher probability that individuals are at a local optima and thus Nash Equilibria are encountered with higher probability.

Kauffman and Johnsen also observed [27] that in a $K = 0$ landscape it takes an exceptionally long time to find the Nash Equilibrium. This length of time can only be shortened with a low C value. This is because there exists only one local optimum for each individual implying that from any configuration, with high probability, an individual can improve its fitness. The fitnesses of the populations fluctuate wildly and the population sizes approach a mean value but never remain constant. On the other hand a high K value ($K = 16, N = 24$) quickly finds Nash Equilibria with little variation due to C .

In researching these various works, several qualities became prevalent. The mathematical derivation of the population growth models is a feature justifiable on its

⁸This notation is introduced here because no notation is given in any previous work.

own merits. Forms of co-evolution are easily distinguished and therefore behaviour related to them is easy to explore and quantify. Unfortunately the models are overly simplified. A range of behaviour cannot be specified within a population. Most importantly the model was made to explore the nature of population growth not explore the nature of co-evolution. Fitness is not even a concept mentioned in population growth models.

Evolutionary Game Theory also has many distinctive advantages and disadvantages. Looking at the nature of individual interactions is really looking at the causes of evolution. Natural selection is a result of competition (between or within species), resource limitations, random luck and behaviour of individuals. By learning to model these things, Maynard Smith and Price have learned to study the source of co-evolution.

NKC models show the diverse possibilities of co-evolution. Kauffman and Johnsen's work shows the results of various interconnected landscapes. It is a comprehensive work that discusses stability in a co-evolutionary setting. By including the Lotka-Volterra work the *NKC* model becomes one of the few works to bridge the gap between population based modeling and fitness based modeling. Unfortunately the fitness relationships between individuals or even populations is not clear. The forms of symbiosis that exist are not constant nor easily described.

A comprehensive survey of the various models of co-evolution was never found; however, there are several interesting compilations. Paul Keddy's book "Competition" [29] is a superb collection and analysis of approaches to modeling population size in competitive relationships. For a more historical view of population growth models, Hutchison's book "An Introduction to Population Ecology" is thorough and consistent in its handling of mathematical notation. In their paper on an EGT model of co-evolution, Kristian Lindgren and Mats Nordahl [35] hint at the diversity of co-evolutionary models. They present several interesting references to prove the diversity of the models. These references along with the references provided here provide a good starting point for research into modeling co-evolution.

4.2 A New Model of Co-evolution

Several goals had to be laid out before a new model of co-evolution could be formed. The chief of these goals is to have a system of modeling that was fully compatible with the descriptive model of symbiosis graphs. This means that it has to be consistent with the definitions of co-evolution, connection, symbiosis, protagonist and antagonist connections. The model is also meant to be usable as an extension to evolutionary computing and is therefore a discrete time model.

4.2.1 Symbiosis Model of Co-evolution

The Symbiosis Model of Co-evolution is a mathematical framework for the purpose of discussing and relating information about specific models of co-evolution. All of the definitions in Chapter 3 apply to this model. The premise of those definitions is that co-evolution is a result of natural selection on individuals in symbiosis.

In modeling an ecosystem several concerns constantly reappear. The method of reproduction (i.e., asexual or sexual), the calculation of an individual's fitness, and genetic representation (e.g. haploid, diploid, triploid...) are several relevant concerns. The symbiosis model of co-evolution is a mathematical model of the interactions between individual's and makes few necessary assumptions about the nature of the system itself. In fact any method of reproduction or genetic representation can be used.

The first important notation regarding the symbiosis model is the concept of the set of all individuals $X = \{x_1, x_2, \dots, x_i, \dots, x_S\}$ where each individual x_i is identifiable by the tag i . For now, the set X will be considered constant; additions and deletions due to births and deaths will be dealt with later. It is assumed that without the interaction of other individuals an individual x_i has a fitness $f_i^a(t)$. A definition of this fitness, known as the absolute fitness, is given in Definition 4.1. Since X contains all individuals there may be individuals of different species. This is accounted for because the absolute fitness function of an individual is mathematically independent of all other individuals. This implies that in an extreme case

every individual could be from a different species.

Definition 4.1 *The absolute fitness of individual x_i at time t , $f_i^a(t)$, is defined to be the individual's fitness without any effects by other individuals. Thus absolute fitness $f_i^a(t)$ is dependent on the genotype and phenotype of x_i , the environment and time t (for a definition of environment see Definition 1.5).⁹*

However the fitness of an individual is affected by other individuals. It is therefore necessary to provide Definition 4.2.

Definition 4.2 *The expressed fitness of individual x_i at time t , $f_i^e(t)$, is defined to be the individual's fitness including the effects of all individuals. The expressed fitness is therefore dependent on the genotype and phenotype of x_i , the environment, time t and all individuals x_j such that $x_j \rightarrow x_i$.*

As mentioned previously, the symbiosis model was intended to be usable as a co-evolutionary extension to evolutionary computing. Since evolutionary computing is a discrete time approach to reproduction and selection events, the symbiosis model is a discrete time model. It is possible to define Equation 4.7 for expressed fitness at time t . In words, the expressed fitness of x_i at time t , $f_i^e(t)$, equals the expressed fitness of x_i at time $t - 1$, $f_i^e(t - 1)$, plus the total change, $C_i(t)$, in the fitness of x_i at time t .

$$f_i^e(t) = f_i^e(t - 1) + C_i(t) \quad (4.7)$$

This enigmatic “total change”, $C_i(t)$, can be broken down into two components: i) changes due to connections to individuals and / or ii) a change in absolute fitness of the individual.

⁹The environment may contain fitness factor which are affected by other individuals. This form of indirect interaction is considered negligible. When these indirect forms of interaction are not present the absolute fitness can be thought of as an individual's fitness without the effects of other individuals.

In the first case all connections, in the symbiosis graph, are modeled to be independent of one another. The total effect of all connections is the sum of all effects by individual connections. Given a connection $x_j - x_i$ then the effect x_j produces on x_i at time t is represented by $c_{ij}(t)$.

In the second case the change in absolute fitness can occur for several reasons. With a change in the environment at time t , the birth or death of an individual are all possible reasons for a change in absolute fitness. It is important to note that death at time t severs the connection between the dead individual x_j and any x_i it was connected to (i.e., $c_{ij}(t+2) = 0, c_{ij}(t+3) = 0, \dots$). What effect the death of the individual has (i.e., $c_{ij}(t+1) = ?$) is up to the person modeling the system. After death the individual becomes a part of the environment (thus the environment changes).

With birth, it is not clear how connections are established. There might be connections established because of inter-species relationships and others because of intra-species social behaviour. With the birth of an individual a new "position" is created in the set of all individuals. With addition of an individual to X , connections are established (by whatever rule the system modeler deems appropriate) and the initial effective fitness is calculated. Assuming that the birth occurs at time t then the expressed fitness of the newborn x_i has been unaffected by other individuals. This implies that the newborn's expressed fitness begins with its absolute fitness $f_i^e(t) = f_i^a(t)$. Since there was no previous fitness the total change is equal to the initial fitness $C_i(t) = f_i^a(t)$.

Using this idea of birth the initial conditions of expressed fitness can be stated. Assume that at time $t = 0$ all individuals are born. Using the conditions stated in the previous paragraph the initial conditions are those stated in Equation 4.8.

$$\begin{aligned} f_i^e(0) &= f_i^a(0) \\ C_i(0) &= f_i^a(0) \end{aligned} \tag{4.8}$$

Using the ideas expressed above Equation 4.9 represents the full formulation for

$C_i(t)$.

$$C_i(t) = \sum_{j=1}^S c_{ij}(t) + (f_i^a(t) - f_i^a(t-1)) \quad (4.9)$$

This leads to Equation 4.10 which is the defining equation for the symbiosis model.

$$f_i^e(t) = f_i^e(t-1) + \sum_{j=1}^S c_{ij}(t) + (f_i^a(t) - f_i^a(t-1)) \quad (4.10)$$

One particularly interesting concern with this model is the implementation of selection. It is assumed, in this model, that selection occurs by the ranking of individual's expressed fitnesses. That is to say probabilities of reproduction and/or survival in the system are directly related to the expressed fitness. There may be several groups (i.e., species) within X that evaluate the probabilities of survival and reproduction independently of one another. There may also be species whose survival probabilities are linked to other individuals but whose reproductive probabilities are independent¹⁰. The main point is that the fitness used in the model is the expressed fitness and that the set of individuals X can contain different species.

Within the symbiosis model there is a wide range of co-evolutionary systems that can be modeled (obviously continuous time models are out). However the type of connection between individuals has not been discussed. There are infinitely many functions for $c_{ij}(t)$ and not all of them could be examined. Equation 4.11 is an example of one such interesting function. This function provides the effect of restoring the individual back towards its absolute fitness whenever its expressed fitness is below the absolute. If this function was $c_{ii}(t)$ for an individual it could be considered a model of an immune system. Such a healing connection's effect on the co-evolution of a system would represent interesting research.

$$c_{ij}(t) = \max(\frac{1}{2}(f_i^a(t-1) - f_i^e(t-1)), 0) \quad (4.11)$$

¹⁰Such species would model dependency of one species on another.

Connection Type	Cause	Effect
Protagonist	$\mathcal{C}_j(t-1) > 0$	$(\mathcal{C}_i(t) = c_{ij}(t)) > 0$
	$\mathcal{C}_j(t-1) < 0$	$(\mathcal{C}_i(t) = c_{ij}(t)) < 0$
Antagonist	$\mathcal{C}_j(t-1) > 0$	$(\mathcal{C}_i(t) = c_{ij}(t)) < 0$
	$\mathcal{C}_j(t-1) < 0$	$(\mathcal{C}_i(t) = c_{ij}(t)) > 0$

Table 4.4: Mathematical Conditions for Protagonist and Antagonist Connections

But under what conditions does the function $c_{ij}(t)$ represent a protagonist or an antagonist connection? This question is easily answered from the definitions of these connections. Considering a system of two individuals x_i and x_j where the only connection in the system is $x_j \rightarrow x_i$. Assuming that the absolute fitness of x_i remains constant then Equation 4.10 for x_i reduces to $f_i^e(t) = f_i^e(t-1) + c_{ij}(t)$. For this case, the connection $x_j \rightarrow x_i$ is summarized by $c_{ij}(t) = f_i^e(t) - f_i^e(t-1)$. Recall that both of the definitions of protagonist and antagonist connections rely on analyzing the sign of the terms $f_j^e(t-1) - f_j^e(t-2) = \mathcal{C}_j(t-1)$ and $f_j^e(t-1) - f_j^e(t-2) = \mathcal{C}_j(t-1)$. Analyzing these terms yields the summary of conditions in Table 4.4.

While many more interpretations of connections could be made it is not necessary because the classic forms of symbiosis studied here are expressible in terms of protagonist and antagonist connections (see Chapter 3). It should be noted that symbiosis graphs can now be extended to describe a specific instance of a symbiosis model. Rather than labeling connections with simple + and - signs they can be labeled with the actual equations $c_{ij}(t)$.

4.2.2 Linear Symbiosis Model of Co-evolution

The Symbiosis Model of Co-evolution is not a model that can be implemented without decisions made on the type of connection model used. The function $c_{ij}(t)$ must be fully specified before an implementation can be completed. This brings back

the problem of the infinite possibilities. Deciding between functions that satisfy the protagonist and antagonist conditions given in Table 4.4 presents infinite choice. This is easily shown by considering that any polynomial of the form $\alpha(\mathcal{C}_j(t-1))^{2n-1}$ where $n \geq 1$ and $n \in \mathcal{N}$ satisfies the protagonist or antagonist conditions depending on α ¹¹.

To decide between the possibilities the principle of simplicity or Ockham's Razor is used. This fundamental approach to scientific inquiry is attributed to William of Ockham¹². Of all of polynomials mentioned above the most basic is the linear form given in Equation 4.12. Using this equation $c_{ij}(t)$ is protagonist when $\alpha_{ij} > 0$ and $c_{ij}(t)$ is antagonist when $\alpha_{ij} < 0$.

$$c_{ij}(t) = \alpha_{ij}\mathcal{C}_j(t-1) \quad (4.12)$$

Using only this type of linear connection for every connection is the criteria for the Linear Symbiosis Model of Co-evolution (or Linear Model of Co-evolution). Given the form of the linear connections it is possible to restate the basic equation of the symbiosis model (Equation 4.10). One improvement that can be made is to produce a vector base format of the formula. Thus let $F^a(t)$ be the vector $[f_1^a(t), \dots, f_i^a(t), \dots, f_S^a(t)]$. Similarly let $F^e(t)$ be the vector $[f_1^e(t), \dots, f_i^e(t), \dots, f_S^e(t)]$ and $\mathcal{C}(t)$ be the vector $[\mathcal{C}_1(t), \dots, \mathcal{C}_i(t), \dots, \mathcal{C}_S(t)]$. Using these definitions with Equations 4.12 and 4.10 produces the defining equation of the linear model given in Equation 4.13.

$$\begin{pmatrix} f_1^e(t) \\ \vdots \\ f_S^e(t) \end{pmatrix} = \begin{pmatrix} f_1^e(t-1) \\ \vdots \\ f_S^e(t-1) \end{pmatrix} + \begin{pmatrix} \alpha_{11} & \dots & \alpha_{1S} \\ \vdots & \ddots & \vdots \\ \alpha_{S1} & \dots & \alpha_{SS} \end{pmatrix} \begin{pmatrix} \mathcal{C}_1(t-1) \\ \vdots \\ \mathcal{C}_S(t-1) \end{pmatrix}$$

¹¹The proof of this general case is left to the reader. The specific case of $n = 1$ is shown in the following paragraphs.

¹²Ockham supposedly wrote "quia frustra fit per plura quod potest fieri per pauciora" which translates "because it is vain to do by more, what can be done by fewer"[22, p. 3].

$$\begin{aligned}
& + \begin{pmatrix} f_1^a(t) \\ \vdots \\ f_S^a(t) \end{pmatrix} - \begin{pmatrix} f_1^a(t-1) \\ \vdots \\ f_S^a(t-1) \end{pmatrix} \\
F^e(t) &= F^e(t-1) + AC(t-1) + F^a(t) - F^a(t-1) \quad (4.13) \\
\text{where } C(t) &= F^e(t) - F^e(t-1)
\end{aligned}$$

Suppose that the absolute fitness of individuals in a system was to stop changing (i.e., $F^a(t) - F^a(t-1) = 0$). It is critical to the analysis of Equation 4.13 to know the answer to: “For what values of A is the statement $\forall i (1 \leq i \leq S \wedge \lim_{t \rightarrow \infty} f_i^a(t) \text{ exists})$ a true statement?”. Essentially, the question asks for the necessary and sufficient conditions of stability of the system. At least sufficient conditions are desirable so that stable systems can be explored without searching through non-stable systems. This relates back to the Red Queen Hypothesis that without external effects a real co-evolutionary system will constantly change (i.e., evolutionary arms races). This begs the question: Do the expressed fitnesses in a real system reach a stable point. do they constantly increase or do they fluctuate wildly? It is assumed, in this thesis, that expressed fitnesses do not constantly increase or decrease but are bounded. It is the opinion of this thesis that a model should ensure the bounds but no model should be disregarded because of behaviour within those bounds.

To express a sufficient condition of stability of the linear model the quantity β must be defined as given in Equation 4.14.

$$\beta = \max \left(\sum_{i=1}^S |\alpha_{i1}|, \dots, \sum_{i=1}^S |\alpha_{ij}|, \dots, \sum_{i=1}^S |\alpha_{iS}| \right) \quad (4.14)$$

Then a sufficient condition for stability of a linear model is $\beta < 1$. The proof of this is given as follows:

To prove that $f_i^e(t)$ is bounded as t approaches ∞ it is only necessary to prove that $G(t) = \sum_{i=1}^S f_i^e(t)$ is bounded. However, to prove this requires Lemma 4.1.

Lemma 4.1 ($D(t) \leq \beta D(t-1)$) *This Lemma is proven by Equations 4.15 to 4.18 which assume $F^a(t) - F^a(t-1) = 0$ and uses Equation 4.7 and the definition*

$$D(t) = \sum_{i=1}^S |\mathcal{C}_i(t)|.$$

$$D(t) = \sum_{i=1}^S |\mathcal{C}_i(t)| = \sum_{i=1}^S \sum_{j=1}^S |c_{ij}(t)| = \sum_{i=1}^S \sum_{j=1}^S |\alpha_{ij} \mathcal{C}_j(t-1)| \quad (4.15)$$

$$= \sum_{j=1}^S \sum_{i=1}^S |\alpha_{ij} \mathcal{C}_j(t-1)| \quad (4.16)$$

$$= \sum_{j=1}^S |\mathcal{C}_j(t-1)| \sum_{i=1}^S |\alpha_{ij}| \quad (4.17)$$

$$\leq \sum_{j=1}^S |\mathcal{C}_j(t-1)| \beta \quad (4.18)$$

Thus it is shown that $D(t) \leq \beta D(t-1)$

Now it is possible to show that $G(t) = \sum_{i=1}^S f_i^e(t)$ is bounded.

Proof:

The upper bound of $G(t)$ is proven by Equations 4.19 to 4.22. These equations are derived from Equation 4.7 and Lemma 4.1.

$$G(t) = \sum_{i=1}^S f_i^e(t) = \sum_{i=1}^S (f_i^e(t-1) + \mathcal{C}_i(t)) \quad (4.19)$$

$$\rightarrow G(t) \leq G(t-1) + \sum_{i=1}^S |\mathcal{C}_i(t)| \quad (4.20)$$

$$\rightarrow G(t) \leq G(t-1) + D(t) \leq G(0) + \sum_{j=0}^t D(j) \quad (4.21)$$

$$\rightarrow G(t) \leq G(0) + \sum_{j=0}^t D(0) \beta^j = G(0) + D(0) \left(\frac{1 - \beta^t}{1 - \beta} \right) \quad (4.22)$$

The upper bound given in Equation 4.22 can be extended to an overall upper bound by taking the limits of both sides. This is shown in Equation 4.23.

$$\begin{aligned} \lim_{t \rightarrow \infty} G(t) &\leq \lim_{t \rightarrow \infty} \left(G(0) + D(0) \left(\frac{1 - \beta^t}{1 - \beta} \right) \right) \\ &\leq G(0) + D(0) \left(\frac{1}{1 - \beta} \right) \end{aligned} \quad (4.23)$$

Figure 4.2: Symbiosis Graph of Expressed Fitness Example

Since the sum of all individuals' fitnesses is bounded from above then each fitness must be bounded from above. Replacing $D(t) = \sum_{i=1}^S |\mathcal{C}_i(t)|$ with $E(t) = -\sum_{i=1}^S |\mathcal{C}_i(t)|$ and using a similar argument the sum of all fitnesses is bounded below and therefore each individual's fitness is bounded from below.

Since the initial condition of $\beta < 1$ leads to the bounds from above and below of each fitness $f_i^e(t)$ then it has been proven that $\beta < 1$ is a sufficient condition for stability of a linear model of co-evolution. $\square$

Linear Symbiosis Fitness Calculation Having given the formula for calculating expressed fitness using the linear model it is appropriate to follow with a specific example of the calculation. Figure 4.2 shows the individuals whose expressed fitnesses are calculated in the example. Table 4.2.2 shows the details of the example with all intermediate values.

Quantity	0	1	2	3	4
$f_i^a(t)$	10	10	10	10	10
$f_i^e(t) = f_i^e(t-1) + c_{ij}(t) + f_i^a(t) - f_i^a(t-1)$	10	14.8	16.8	17.72	17.32
$c_{ij}(t) = \alpha_{ij}C_j(t-1)$	0	4.8	2.0	0.92	-0.4
$C_i(t) = f_i^e(t) - f_i^e(t-1)$	10	4.8	2.0	0.92	-0.4
$f_j^a(t)$	12	12	12	10	10
$f_j^e(t) = f_j^e(t-1) + c_{ji}(t) + f_j^a(t) - f_j^a(t-1)$	12	17	19.4	18.4	18.86
$c_{ji}(t) = \alpha_{ji}C_i(t-1)$	0	5	2.4	1.0	0.46
$C_j(t) = f_j^e(t) - f_j^e(t-1)$	12	5	2.4	-1.0	0.46

Table 4.5: This example shows how the expressed fitnesses of individuals x_i and x_j are calculated. The table begins at the birth of both individuals and goes until time $t = 4$. The symbiosis graph for this example is shown in Figure 4.2.

Chapter 5

Implementing Co-evolution in GAs

There are a number of decisions that have to be made when implementing co-evolution into GAs. These decisions range from the large range of parameters available to a regular GA to the different forms of co-evolution implemented. To perform a comprehensive examination of the parameters of a GA is a career goal of many prominent researchers and is beyond the scope this thesis. This combined with the attempt to model co-evolution into a GA expands the search space to overwhelming proportions. This chapter discusses the implementation used to experiment with the linear symbiosis model. The goal of this chapter is to describe the system with enough detail for the reader to implement an equivalent system while describing the rationale behind the more critical decisions about the implementation.

Section 5.1 deals with how life and death affect expressed fitness. This explains the model of life and death used here and prepares the reader for a description of the implementation. In Section 5.2 the object model of the implementation is given and the required functionality is described. Section 5.3 introduces the forms of co-evolution used throughout the experiments. Finally, Section 5.4 outlines the parameters used in the implementation of the GA.

5.1 Linear Model Concerns

Besides the details of implementing the expressed fitness of a living individual, there are a number of concerns dealing with the birth and death of individuals¹. These primary concerns are how the death of an individual in symbiosis affects its partners, how a newborn affects expressed fitnesses and how the system changes as a whole because of births and deaths.

Suppose a child x_j is born at time $t + 1$. At the time of birth the expressed fitness of x_j should be equal to the absolute fitness of x_j plus any effects felt at time t . However, since the child was not alive in the previous time then $C_j(t) = 0$. The remainder of the equations apply. In the model explored here each child is assigned its connections at birth and they remain constant throughout its life. Should any individual die then the new child that is created to replace it will inherit the dead individual's connections. This is only possible because, in the implemented GA, the population size is constant.

Death and its effects are also critical to the implementation of the model. Consider Equation 4.10 from the linear symbiosis model. Suppose at time t an individual x_j was alive and affecting individual x_i . If the individual dies then at time $t + 1$ individual x_j is not alive. This means that the change $C_j(t)$ in x_j between times $t - 1$ and t will not affect individual x_i at time $t + 1$ (i.e., $C_j(t) = 0$, regardless of $f_j^e(t)$ and $f_j^e(t - 1)$).

Suppose that an individual x_i is in symbiosis with x_j and at time t individual x_j dies (i.e., at time t individual x_j exists and at time $t + 1$ it doesn't). Further suppose that at time $t + 1$ a new individual is born and takes x_j 's place. In essence the new individual becomes the new x_j . Since the death and birth both indicate that $C_j(t) = 0$ then there is nothing further to model. To clarify this point suppose the individuals x_i and x_j are connected as shown in the symbiosis graph of Figure 5.1. In this implementation the fitness of the individuals would be calculated as shown in Table 5.1.

¹See Section 5.2 for details on implementing the expressed fitness.

Quantity	$t - 1$	t	$t + 1$	$t + 2$	$t + 3$
$f_i^a(t)$	10	10	10	10	10
$f_i^e(t) = f_i^e(t - 1) + c_{ij}(t) + f_i^a(t) - f_i^a(t - 1)$	19.6	20.2	20.2	21.4	21.4
$c_{ij}(t) = \alpha_{ij}C_j(t - 1)$	1.6	0.6	0	1.2	0
$C_i(t) = f_i^e(t) - f_i^e(t - 1)$	1.6	0.6	0	1.2	0
$f_j^a(t)$	5	5	11	11	11
$f_j^e(t) = f_j^e(t - 1) + c_{ji}(t) + f_j^a(t) - f_j^a(t - 1)$	13.5	14.3	11.3	11.3	11.9
$c_{ji}(t) = \alpha_{ji}C_i(t - 1)$	2.5	0.8	0.3	0	0.6
$C_j(t) = f_j^e(t) - f_j^e(t - 1)$	2.5	1.5 0	3	0	0.6
Event		Death of x_j	Birth of new x_j		

Table 5.1: The values in the column time $t - 2$ are assumed to have been taken from midpoint in the individuals' lives. The event of death and subsequent birth should be noted as different from the case where an individual's absolute fitness changes (See Table 4.2 and Figure 4.2). It is important to note the change in $C_j(t)$ to 0 once the death had occurred. The overstruck value is the value that would have been appropriate had the death not occurred³.

Figure 5.1: Symbiosis Graph of Birth/Death Example

This is just one possible model of birth and death. It was chosen because it represents a reasonable first attempt at exploring the intricacies of co-evolution without unnecessary complications. In modeling a specific form of co-evolution the assumptions made above may not be applicable. It is reasonable that the death of an individual could be beneficial to another individual (e.g. the death of prey is often beneficial to the predator). Conversely the death of an individual might be detrimental to another individual (e.g. the death of a co-dependent is severely detrimental to the survivor). In these cases $C_j(t) \neq 0$. These alternatives are discussed further in the Future Work section of Chapter 7.

5.2 Object Model

Since one of the main goals of this work is to compare a co-evolutionary GA to a normal GA both should be implemented with the same objects. This ensures that the only differences are in the calculation of the expressed fitness of an individual. For a regular GA the expressed fitness is always the absolute fitness. However, for the co-evolutionary GA the linear symbiosis model was implemented. Thus the Object Model used in this thesis has to be general enough to include both regular and co-evolutionary techniques.

As with all good object-oriented design it is important to consider the extendibil-

ity of the Object Model. While this thesis concerns itself only with the implementation of a GA, the object model used should not depend on specific types of population control. By allowing this flexibility in the model the goal was to create a system that could be later extended to include other forms of Evolutionary Computation.

Finally, when creating the implementation it was considered important to use as natural a model as possible. This enables other people to understand the system quickly, either for analysis or extension purposes. The final structure chosen is shown in an OMT⁴ diagram in Figure 5.2. Details of functionality are described in the following paragraphs.

World The *World* class is instantiated only once in a program. It is the task of the *World* object to synchronize the evolution of multiple populations. To do this the *World* instructs each *Population* in turn to perform a generation. Once all *Populations* have advanced a generation then the expressed fitnesses of the *Individuals* in each *Population* can be calculated and updated. In this manner, *Individuals* in different *Populations* can affect one another in a controlled and analyzable fashion.

To ensure that the modularity of objects is not compromised any object requiring information from a *Population* must request it through the *World* object that contains that *Population*.

Population A *Population* provides all of the functionality required to evolve a collection of *Individuals*. The *Population* size, number of elite *Individuals* that survive into the next round and the maintenance of the sorted collection of *Individuals*⁵ are all handled by a *Population*. The *Population* also maintains a set of statistics on its *Individuals* and sends these statistics to any output

⁴OMT stands for Object Model Techniques, which is a system of Object-Oriented Program Development created by Rumbaugh in 1985 at General Electric. The details of this system are available in Rumbaugh's book [60].

⁵The *Individuals* in a *Population* are sorted by their expressed fitnesses. This is discussed further in Section 5.4.

Figure 5.2: This diagram represents the objects and their basic relationships as implemented.

stream. The *Population* must also determine which *Individuals* are to mate and which *Individuals* will be replaced by children.

In the case of co-evolution the *Population* object provides each *Individual* with its collection of *Connections*. Essentially, the *Population* and the “position” that an *Individual* is born into dictates what *Individual(s)* it is connected to. In this model only *Individuals* within the same *World* object can be connected together. This is to ensure proper synchronization of evolution.

The *Population* also acts as an interface to the *Individuals* that it contains. Thus any object requiring knowledge about an *Individual* must pass its request through the *Population*.

Individual Every *Individual* is a member of one and only one *Population*. At any given time an *Individual* has an age, absolute fitness and expressed fitness. As shown in Figure 5.2 the *Individual* contains a *Genome* and zero or more *Connections*. The *Individual's* *Genome* is a solution to its *Population's* *Problem*. The *Individual* only uses the functionality defined in the abstract *Genome* and *Problem* classes. This is important because it allows for easy extension of the model to include different *Problems* and/or *Genomes*.

There are two cases of reproduction that were implemented. In the first case the *Individual* is born without parents. In this case the *Individual* simply queries the *Problem* and a random *Genome* of the appropriate type is returned. The second case is the birth of a new *Individual* with parents. The new *Individual* queries the *Problem* for a new *Genome* of the appropriate type, then the new *Genome* initializes itself using its parents' *Genomes*.

At birth an *Individual's* expressed fitness equals its absolute fitness plus any changes experienced at birth. To obtain its absolute fitness at any time the *Individual* does not need to have any functionality specific to its *Genome* or *Problem*. Instead the *Individual* simply queries the *Problem* to calculate its *Genome's* fitness.

The *Connections* that are contained in the *Individual* are the *Connections* that

affect the *Individual*. This was done so the *Individual* could simply query its *Connections* to determine the sum of the effects on itself at any given time.

Connection The only functionality that a general *Connection* must have is to provide the effect associated with the connection at the current time (i.e., $c_{ij}(t)$). Since the possible number of *Connections* types are very large, *Connection* is necessarily an abstract class that provides the interface for getting the effect at any given time. In this implementation a *Connection* is only between *Individuals* in the same *World*. This means that the *Connection* knows which *World* it is in. Any requests by a *Connection* to an *Individual* are passed through its *World* object. Since a variety of *Connection* types are possible the *Connection* also has a description and a tag identifying what type of *Connection* it is.

Linear Connection The *Linear Connection* class represents a connection between an affecting *Individual* and an affected *Individual*. In a *Linear Connection* object it is required to calculate the effect at any given time (i.e., $c_{ij}(t)$). Thus at time t the *Connection* requests $C_j(t-1) = f_j^e(t-1) - f_j^e(t-1)$ from *Individual* x_j . Each *Linear Connection* has a weight α_{ij} associated with it. Then the effect produced by the connection at time t is simply $\alpha_{ij}C_j(t-1)$.

The *Linear Connection* is the backbone of the linear symbiosis model of co-evolution. However, this is not the only type of connection possible and some suggestions are made in Chapter 7.

Genome This class is an abstract class that provides the interface that the *Individual* uses to gain access to information from an arbitrary instance of *Genome*. Since there are a variety of types of *Genomes* each instantiation must be able to provide a description of itself both numerically and in text. This allows a check to be performed before a *Problem* tries to use a *Genome* as a solution. Each *Genome* must also be capable of using its two parent *Genomes* to initialize itself. Since *Problems* evaluate the absolute fitness of a *Genome*, each type of *Genome* must provide an functionality required by its problem (e.g., a binary string genome must provide read access to its binary string).

Form of Co-evolution	Individuals Required
Adaptism	1
Mutualism	2
Predation	2
Competition	2

Table 5.2: All of these forms of co-evolution involve feedback. For the definitions of each form see Chapter 3.

As shown in Figure 5.2, this implementation has two different types of *Genomes* Binary Vector Genome and TSP Path Genome which are described in detail in Section 6.2.

Problem Problem is another abstract class that can create appropriate random *Genomes* and evaluate the absolute fitness of *Genomes*. Five sub-classes of *Problems* have been implemented. Of these five, one (the Binary Vector Problem) is an abstract class and provides the necessary binary string/vector functionality for its sub-classes. The other four sub-classes (TSP Problem, Rosenbrock's Function, Griewangk's Function and Holland's Royal Road Function) are all concrete classes. Each of the *Problem* sub-classes are described in Section 6.1.

5.3 Forms of Co-evolution Examined

Only a select group of co-evolutionary forms are studied in this thesis. In the article by Robertson and Grant [57] it is clearly noted that co-evolutionary systems with feedback are of the more interesting forms. Of the various symbiosis graphs that could have been chosen only those basic forms displaying feedback were chosen. The full list of forms studied is given in Table 5.3.

Having decided on the forms of co-evolution to be studied the next step was to

Figure 5.3: This symbiosis forest represents the individuals of a population co-evolving with Adaptism.

decide how the population was to be inter-connected. It was decided that in any experiment only one of the basic forms of co-evolution would be present. This was done to allow clear analysis of each form. Fortunately the forms of co-evolution studied (see Table 5.3) fall into two categories. Adaptism falls into its own category because every individual is only connected to itself. Thus the symbiosis forest of the population is given by Figure 5.3.

The other three forms of co-evolution (Mutualism, Predation and Competition) require two individuals to be connected to each other. Since this is an initial investigation, each individual is only in symbiosis with one other individual. This allows an examination of the basic forms of co-evolution without added complications. The symbiosis forest for a single population, using any of these three forms of co-evolution, is shown in Figure 5.4.

In the implementation of these symbiosis forests it is assumed that every individual in a population has a unique position i^6 . Based on i the individual is given a collection of connections by its population. For the purpose of analysis the magnitudes of the constants α_{ij} are all equal. In this way the weights of the connections could be varied from experiment to experiment to determine the effect of the magnitude (i.e., strength) of a connection.

⁶This position never changes during the lifetime of the individual. It is an absolute position regardless of the individual's expressed fitness. It is also necessary to ensure that the population can reference an individual by its position and that an individual knows its position.

Suppose x_i is in symbiosis with x_j And $j = i + 1$:

Mutualism

$$\alpha_{ij} > 0$$

$$\alpha_{ji} > 0$$

Predation

$$\alpha_{ij} > 0$$

$$\alpha_{ji} < 0$$

Competition

$$\alpha_{ij} < 0$$

$$\alpha_{ji} < 0$$

Figure 5.4: This symbiosis graph represents the individuals of a population co-evolving with Mutualism, Predation or Competition. The conditions for each form of co-evolution are reiterated from Section 4.2.2.

5.4 Genetic Algorithm Concerns

Just as all forms of co-evolution could not be tested neither could all of the forms of Genetic Algorithms. This thesis does not attempt to measure the effect of varying GA parameters on a co-evolutionary GA. Instead this thesis examines the behaviour of co-evolution in a specific GA. In order to examine the behaviour of co-evolution in a GA it was necessary to pick the form of the GA to be implemented.

Since the GAs is a general optimization technique it was decided that the GA should not be specially altered to suit any of the problems dealt with here. This meant that conventional GA parameters would be used wherever possible and no special aid would be given to the regular GA. This helped to ensure that the results from the GA and the co-evolutionary GAs could be compared.

Unfortunately there are very few agreed upon conventional GA parameters for a general problem. Most of the GA parameters were chosen by virtue of common usage in GA literature. However, in the case of reproduction selection the decision was made based on a survey paper by Baker [4]. Baker concluded that his Rank Based Selection allowed the greatest genetic diversity within a population and thereby controlled premature convergence. The implementation for this thesis used this Rank Based Selection technique as it was described by Baker [4].

In GAs there are two fundamentally different approaches to Survival. Either some individuals survive into the next generation (i.e., it is a Steady-State GA) or none survive (i.e., it is a Generational GA). If co-evolution is the form of evolution that results in the presence of symbiosis then individuals must survive long enough for the symbioses to have an effect. For this reason a Steady-State GA was chosen for the implementation. Fortunately, there is evidence that Steady-State GAs can “find as good or better solutions in much less time than Generational GAs” [65, p. 100]. In this implementation a fixed percentage of the population was allowed to survive into the next generation. All individuals were ranked by the population according to their expressed fitness and the ones with the highest expressed fitness were allowed to survive. For the GA without co-evolution the expressed fitness was

simply the absolute fitness.

The replacement rate of a Steady-State GA (i.e., how many individuals are replaced every generation) is a point of contention amongst the GA community. Some favor the extreme of this parameter with a replacement rate of one individual⁷. This allows good individuals a higher probability of reproduction. In this implementation a lower replacement rate implies a larger effect of co-evolution. This is because there are more active connections with a higher replacement rate and the length of the average individual's life will be much longer thereby increasing the sum of the effects on an individual. Since this represents an initial investigation it was desired to see the effect of a minimal amount of co-evolution on the system. This would allow the effects to be noticeable without being overwhelming or distorted. For this reason the replacement rate was set to 90%. Thus only 10% of the previous generation was allowed to survive into the following generation.

⁷Specifically the Genitor Algorithm adds only one individual, thereby removing only one individual, per "generation" and has proven quite successful.

Chapter 6

Problems, Genomes and Experiments Implemented

The choice of problems to use during experimentation was not easy. The problems had to represent a wide diversity of types while presenting different challenges to a GA. Specifically problems were sought that evoked three different behaviours from the GA:

- 1) Fast and accurate convergence with subsequent loss of genetic diversity.
- 2) Fast and inaccurate convergence with subsequent loss of genetic diversity.
- 3) Slow convergence and sometimes inaccurate convergence.

It was hypothesized that since the GA behaved differently on these types of problems that the co-evolutionary GA might also behave differently. It was hoped that by finding problems that fit these behaviour types a larger range of co-evolutionary behaviour would be observable. The following 4 problems cover the three different behaviours within a GA and all except one (Rosenbrock's Function) represent difficulties for traditional optimization techniques.

6.1 Problems

6.1.1 Rosenbrock's Function

Rosenbrock's function has a long history in optimization theory and GAs. The reason this function (See Equation 6.1) is interesting is because it is a simple two dimensional, non-linear, non-separable equation whose local minimum is known. In the implementation used here the function has be modified to be the negative of Rosenbrock's Function.

$$F2(y_1, y_2) = 100(y_1^2 - y_2)^2 + (1 - y_1)^2 \quad (6.1)$$

Because Rosenbrock's function is non-linear and non-separable normal line search techniques are largely ineffective. However, this function can be solved using a special adaptation of linear search [70, p. 5].

To implement Rosenbrock's Function each individual must represent a two dimensional vector. The vector space, bit precision and formula used in this implementation are shown in Table 6.1.

Parameter	Value
Maximum (y_1, y_2)	(2.048, 2.048)
Minimum (y_1, y_2)	(-2.048, -2.048)
Total Bits	32
x_i	(y_{i1}, y_{i2})
$f_i^a(t)$	$-100(y_{i1}^2 - y_{i2})^2 - (1 - y_{i1})^2$

Table 6.1: These are the parameters used to implement Rosenbrock's Function in this thesis. The "Total Bits" is the total number of bits used to represent y_{i1} and y_{i2} in each individual. The maximum fitness attainable is at (1.1) and is equal to 0.

Rosenbrock's Function is considered to be a problem of the first type mentioned. Typically using a GA produces good results quickly; however, after the fitness stops

improving the genetic diversity continues to decrease. This is also the behaviour found in the implementation and is further commented on in Section 6.3.2.

6.1.2 Griewangk's Function

In the GA literature, Griewangk's Function is far less common than Rosenbrock's function. Described and analyzed by Whitley, et. al. [70], Griewangk's Function is a scalable, non-linear, non-separable function that is hard¹ to optimize in lower dimensions.

Since Griewangk's Function is traditionally a minimization problem the negative of Griewangk's Function was used in this implementation. All of the parameters used in this implementation are seen in Table 6.2. It was hoped that Griewangk's Function would be of a similar nature to Rosenbrock's Function. While the system would find results at a different accuracy the representation of solutions and everything else could be the same. This hope was verified as the Regular GA rapidly found accurate results and then having found good results continued to decrease the genetic diversity of the population.

6.1.3 Holland's Royal Road

In 1991 Holland, et. al. produced a paper describing the first Royal Road function [44]. The idea behind the Royal Road function was to create a function that the GA could optimize but that other optimization techniques could not optimize². However, this original function was shown to be inadequate to its purpose and in 1993 Holland produced another Royal Road Function [20]. This new Royal Road function is the one presented here and, to the best of the author's knowledge the optimum has not been found by any optimization technique other than GAs.

¹Whitley, et. al. [70] describe the techniques and parameters that permit easier optimization of Griewangk's Function.

²Specifically the purpose of the Royal Road Function was to defeat hill climbers that did not use the crossover operator of GAs.

Parameter	Value
Dimensions	2
Maximum (y_1, y_2)	(511, 511)
Minimum (y_1, y_2)	(-512, -512)
Total Bits	32
x_i	(y_{i1}, y_{i2})
$f_i^a(t)$	$-1 - \sum_{j=1}^2 \frac{y_{ij}^2}{4000} + \prod_{j=1}^2 (\cos(\frac{y_{ij}}{\sqrt{i}}))$

Table 6.2: These are the parameters used to implement Griewangk's Function in this thesis. The "Total Bits" is the total number of bits used to represent x and y in each individual. The maximum fitness attainable is at (0,0) and is equal to 0.

The main idea behind the Royal Road Function is to calculate a fitness value of a binary string. Each string contains 2^k non-overlapping regions each of length $b + g$. To calculate the fitness of a given binary string x the number of 1's bits in the first b bits of each region r are counted (Denoted: $\sigma(x, r)$). Using $\sigma(x, r)$ the first part of the fitness f_p is calculated by the Equation 6.2.

$$f_p(x) = \sum_{j=1}^{2^k} f_p(x, r)$$

$$f_p(x, r) = \begin{cases} v\sigma(x, r), & \sigma(x, r) \leq m^* \\ -v(\sigma(x, r) - m^*), & m^* < \sigma(x, r) < b \\ 0, & \sigma(x, r) = b \end{cases} \quad (6.2)$$

The second (or bonus) part of x 's fitness is denoted $f_b(x)$. This bonus fitness consists of k levels. At the first level $f_b(x)$ is increased by u^* if there is a region r whose $\sigma(x, r) = b$. Then for every other region whose $\sigma(x, r) = b$ the fitness $f_b(x)$ is increased by u .

The second level performs a similar calculation except instead of simply requiring $\sigma(x, r) = b$ the requirement is $\sigma(x, r) = b$ and $\sigma(x + 1, r) = b$ where $x = 0(\text{mod}2)$.

Parameter	Value
k	4
b	8
g	7
m^*	4
v	0.02
u^*	1.0
u	0.3
$f_i^a(t)$	see description or [24]

Table 6.3: These are the parameters used to implement Holland's Royal Road Function in this thesis. Using these defaults the maximum fitness is 12.8 while the minimum is -0.9.

In each subsequent level the requirement involves twice the number of regions as the previous level. The reader is invited to consult [24] for a more detailed definition.

The entire fitness of x is then calculated to be $f(x) = f_b(x) + f_p(x)$. The parameters used in this implementation are those originally given by Holland and are shown in Table 6.3. It was included because it was hoped that it fell into the second type of behaviour. Experimentation showed that the Royal Road Function was not fully optimized by a GA and that the system lost genetic diversity thereby stopping its progress.

6.1.4 Traveling Salesman Problem

The Traveling Salesman Problem (TSP) is an interesting NP-complete graph theory problem³. Each problem has a set of cities (i.e., 2-D points) and the problem is to minimize the distance traveled by a salesman visiting all of the cities and returning

³This implementation dealt only with the Euclidean 2-D TSP. Subsequently all references to the TSP will be to the Euclidean 2-D TSP.

TSP Problem	Number of Cities	Maximal Fitness
Eil51	51	-426
Eil76	76	-538
Eil101	101	-629

Table 6.4: The above are the TSPs used. These problems each have known optimum solutions and this is represented in the above table.

to the original city. The distance between cities is assumed to be the distance between the cities rounded to the nearest integer⁴. Since the TSP is a minimization problem the negative total distance was used as a measure of fitness and the fitness was maximized.

A total of three different TSP problems were analyzed (See Table 6.4). Each of these three came from the TSPLIB (the standard set of TSP problems maintained by: Gerhard Reinhold, Universität Heidelberg) and each represents a larger problem. Since the GA has shown itself to be a slow and sometimes inaccurate convergent process on these problems, then these problems satisfy the third form of GA behaviour.

6.2 Genomes

6.2.1 Binary Vector Genome

The Binary Vector Genome serves as a solution to all of the sub-classes of the abstract class Binary Vector Problem. In this implementation these sub-classes were: Rosenbrock's Function, Griewangk's Function and Holland's Royal Road Function. Essentially the Binary Vector Genome is a single binary string that can implement a vector or simply function as a binary string.

⁴This method of calculation is considered standard by the academic community interested in the TSP and is described in the TSPLIB(a package of standard test cases provided on the Internet).

This divides the class into two clear functionalities: that required to solve problems like Rosenbrock's and Griewangk's Functions and that required to solve Holland's Royal Road. Since the data for the genome is a binary string⁵ then to implement a vector a mapping is required from the binary string to the vector format. Since each problem may require a different domain, the domain $[max, min]$ must be stored in each instance of the genome⁶.

With each genome containing a binary string and its domain the conversion from binary string to real valued vector can be performed. First the genome breaks the binary string into equal segments, one for each dimension of the vector. For each dimension the binary string segment is considered to be an integer written in base two. These integers are converted to base 10 and then the mapping begins. Since there was a maximum number of bits per component there was a maximum possible integer which is mapped to the maximum of the problem's domain. Since the minimum of the integer was 0 (i.e., all zeros in the binary string segment) then 0 will map to the minimum of the problem's domain. With these two mapping points defined a linear mapping from the integers to the domain is established. Using this mapping it is possible for the Binary Vector Genome to serve as a real value vector genome. For Holland's Royal Road Function the Binary Vector Genome must simply return the binary string when it is requested to do so.

The Binary Vector Genome is also required to initialize itself given "parent" Binary Vector Genomes. Two different types of operators are used. The crossover operator takes two parents and creates a child. Single point, 2-point, 4-point and uniform crossover all operate on the principle displayed in Figure 6.1. The copy operator, which is applied when crossover does not occur, simply takes one parent and copies its genome into the child. As the name indicates the copy operator simply took one parent and copied the parent's genome into the child. For any operator, whenever a bit is written into the child's genome there was a probability, called the mutation rate, with which it would be changed from a 1 to a 0 or vice-versa.

⁵The length of the binary string is specified at instantiation.

⁶In this implementation each component of the vector had the same domain.

Figure 6.1: Each Crossover point is chosen at random without replacement.

Since a goal of this thesis is to maintain genetic diversity in the population a statistical measure of this diversity is taken. To measure this diversity the Hamming distance between two Binary Vector Genomes was implemented. Given the binary string from two genomes the Hamming distance is the number of bits that are different between the binary strings.

This implementation of the Binary Vector Genome is the typical implementation required in a GA. One possibility would have been to use Gray coding to transform the binary strings into integers. Whitley, et. al. [70] showed that Gray coding produces better results than the encoding used here when optimizing Griewangk's function. However, Gray coding is not used here because the results of the encoding previously described are already quite good.

6.2.2 TSP Path Genome

The TSPs implemented require a genome that is a tour of the cities (i.e., points) in the problem (See Section 6.1.4). That is, every solution to the TSP has to be a listing of all the cities, in the order visited. This is easily represented by a linked list of each of the cities (each city is assumed to be represented by a number from 0 to N where N is the number of cities in the problem minus one). Unfortunately a different operator than the traditional crossover operators⁷ was required because the latter do not guarantee valid tours. Consider the six-city tours (0-2-4-1-3-5) and (0-2-3-1-4-5). If these two tours are crossed at the third point then the child tour would be (0-2-4-1-4-5). This is not a valid tour because city 3 is not visited and city 4 is visited twice.

Having decided that the linked list representation is an efficient method of representing a tour it only remains to find a crossover operator that always finds a child that is valid. Fortunately there is a large body of work in the field and Starkweather, et. al. [63] compares a variety of the operators. Of the four operators that achieve the shortest tours the Order Crossover attributed to Davis is the quickest

⁷The traditional operators are those operators in Figure 6.1.

Parent 1	Parent 2	Child
0	4	1
2	1	0
3	5	2
5	0	5
4	2	4
1	3	3

Table 6.5: In the above example the crossover points are 4 and 6. This means that cities 5 and 4 are copied into the child in their positions. The remainder of the cities are copied in order (3,1,0,2) from parent 2.

to perform. By Starkweather's evaluation this operator only converged slower than edge-recombination. Since its performance is relatively good it was chosen to be the crossover operator used here.

For In this operator two crossover points are chosen and the segment between the points is copied from the first parent into the child. Then, starting at the second crossover point, in both the child and the second parent, the remainder of the cities not in the child are copied, in order, into the child. An example of this form of crossover is given in Table 6.5. Unlike the Binary Vector Genome no mutations are implemented.

6.3 Experiments

6.3.1 Description

With the forms of co-evolution and the problems described all that remains is to describe the parameters of the GA (i.e., mutation rates, crossover rates, population size...) and the experimental procedure. The parameters of the GA were set using the parameters given in Table 6.6. With the exception of the TSPs the use of 100

Type of Problem	Form of Co-evolution	Crossover Operator	Population Size	No. of Survivors	Mutation Rate	Crossover Rate
Rosenbrock, Griewangk and Royal Road	Regular GA	1 Point	100	10	0.001	0.6
		2 Point	100	10	0.001	0.6
		4 Point	100	10	0.001	0.6
		Uniform	100	10	0.001	0.6
	Co-evolution	Uniform	100	10	0.001	0.6
TSPs	All	Order	100	10	N/A	1.0

Table 6.6: Most of the parameters are implemented to be the same across experiments. The important variations are the problem type, connection strengths and forms of co-evolution.

individuals as a population size is quite common. However for a TSP it is slightly larger than normal for a 51 city problem and about normal for the 101 city problem [63].

Uniform crossover was chosen throughout the co-evolutionary experiments with the binary vector problems because it represents a good initial approach to a problem. It should be mentioned that there is no magic crossover, which crossover is better will depend on which function is being optimized. Jones gives an excellent discussion on operators and different optimization functions and highlights some of the difficulties in selecting crossover operators [24].

For those experiments involving co-evolution decisions had to be made regarding the weights of the connections (α_{ij}). As mentioned in Section 5.3 all of the weights, in a population, had the same magnitude. This allows the system to be uniform and analyzable on a large scale. Since in each of the models every individual affects only one individual then the magnitudes of the weights may vary from $0 \leq \alpha_{ij} < 1$. It was desired to see the changes in behaviour when the strength (i.e., weights) of the connections was varied from very weak to very strong (i.e., increase the magnitude). It was hoped that this would provide the variation from regular GA behaviour

($\alpha_{ij} = 0$) to strong co-evolutionary behaviour. The weight magnitudes used tried to represent as much of the behaviour as possible. Table A.1 shows all of the α s tested for each form of co-evolution.

6.3.2 Results and Discussion

Before the system was run, a hypothesis had to be made about which measures would be useful in analyzing the system and measuring its performance. Some standard measures were obvious; the best fitness⁸ of every individual (best ever fitness) and the best fitness of current individuals (current best fitness).

Since one of the goals of this thesis is to remove the loss of genetic diversity present in a normal GA some measure of genetic diversity needed to be recorded. It was decided that only the genetic diversity of the survivors would be measured. In this way the amount of genetic diversity that survives in the system was recorded every generation.

For the Binary Vector Genomes the chosen measure of genetic diversity was the average Hamming distance⁹ of the survivors to the survivor with the best fitness. Unfortunately no good measure of genetic diversity for the TSP Path genome exists so.

In using the expressed fitness to determine survival and reproductive fitness it was hoped that individuals whose absolute fitness is mediocre would be able to survive and maintain genetic diversity. This means that more individuals from the early stages of the GA would have to survive into later stages of the GA. Thus an important key to the success of the co-evolutionary system would be the aging of the surviving population. Thus it was determined that the average age of the survivors would be recorded every generation.

Before describing the specific results for the different problems a description of behaviour common to all problems is warranted. Since the effects on expressed

⁸The fitnesses referred to in this section unless otherwise noted are the absolute fitnesses.

⁹The Hamming distance between two binary strings is the number of bits that are different between the two strings.

fitness are cumulative an individual's expressed fitness may become higher than the global optimum of the absolute fitness. This leads to two possible stages in a co-evolutionary GA.

In the first stage, during the early generations, the co-evolutionary GA behaves similarly to a regular GA. Variations in the form of co-evolution and in α dictates variation in the best fitness ever achieved. However the degree of variation in the best fitness ever achieved is problem dependent and will therefore be discussed in the results for each problem.

After the co-evolutionary GA has converged for a while, the amount of change introduced by the new individuals over the individuals being replaced is lower (i.e., the average $C_i(t) = f_i^e(t) - f_i^e(t-1)$ is smaller). This implies that it is less frequent for new individuals to survive into the next generation. At some point in the co-evolutionary GA the value of $C_i(t)$ is too small to allow new individuals to survive. It is at this point that the co-evolutionary GA changes to its second stage of behaviour. From this point onward the surviving population remains constant (with only infrequent changes). This means that after this point the genetic diversity remains constant. Improvement in the best ever fitness comes only because of the constant random recombination of the existing genetic diversity into new individuals. Thus the second stage of behaviour is equivalent to a random search.

The nature of the change between the two behaviours is dependent on the form of co-evolution, the strength of the connections, the problem structure and the form of crossover used. The specifics of these differences are described in the following sections on the results of each problem.

Binary Vector Functions For Rosenbrock, Griewangk and the Royal Road Functions the results show that co-evolutionary GAs can outperform the regular GA. That is, the best individual found (in absolute fitness) by the co-evolutionary GA is on average better than that found by the regular GA. This was achieved by the preservation of individuals from previous generations. The four different forms of

co-evolution tested¹⁰ show a clear ordering of the average age of survivors. Figures A.5, A.11 and A.17 show that the average age of a survivor is consistently between different forms of co-evolution. At the 100th generation the average age of survivors is higher for Adaptism than Mutualism which is higher than for Predation which in turn is higher than Competition. The reason for this ordering can be inferred by examining the expressed fitness of individuals, $f_i^e(t)$ and the changes in expressed fitness of individuals $C_i(t)$.

In the GA implemented an individual that is born, and survives, must be replacing an individual with a lower expressed fitness. This is because survival is based on the ordering of individuals by expressed fitness. When an individual survives its expressed fitness is high enough to survive while the individual that it replaced did not have a high enough expressed fitness to survive. Since $C_i(t) = f_i^e(t) - f_i^e(t-1)$ then $C_i(t) \geq \text{zero}$ (remember that for non-survivors $C_i(t) = 0$). The only exception to this fact is the initial condition at the birth of the population: $C_i(0) = f_i^a(0)$. Given these facts it can now be shown why the trend in average age exists.

With Adaptism each individual that survives has its expressed fitness changed by $c_{ii}(t) = \alpha_{ii}C_i(t-1)$. Since $C_i(t-1) \geq \text{zero}$ and $\alpha_{ii} > 0$ this implies that $c_{ii}(t) \geq 0$. Thus surviving individuals have their expressed fitnesses raised (in decreasing amounts) with each generation. At some point the new individuals, whose $f_i^e(t) = f_i^a(t)$, cannot achieve the expressed fitness achieved by the surviving individuals (the survivors' expressed fitnesses may be above the global optimum for the absolute fitness). Once this occurs the survivors will not be replaced and the average age of the survivors starts to climb dramatically.

Since, in Mutualism, all $\alpha_{ij} > 0$ the conditions are very similar to Adaptism and similar behaviour is displayed. The difference between the two lies in the necessity for both individuals in a pairing to survive at the same time to increase the expressed fitnesses above the global optimum for the absolute fitness. Since this won't always occur, the average age of the survivors won't start to climb until after the point that Adaptism does.

¹⁰Again: Adaptism, Mutualism, Predation and Competition were tested.

In Predation a slightly different arrangement occurs. The survivors do achieve an expressed fitness higher than the absolute fitness. Since half of the individuals are affected by a connection with $\alpha_{ij} < 0$, then surviving pairs are even less likely than in Mutualism.

It should be noted that this analysis implies that with increasing α all three of these forms of co-evolution (Adaptism, Mutualism and Predation) should increase the expressed fitness even further and faster. This does happen and as a result the higher the α the earlier the average age of survivors starts to climb. This trend that as α increases the average age of survivors increases, implies that the surviving population stops changing earlier and earlier in the experimentation. This follows because for the average age of the survivors to be older fewer new individuals would have survived. Since genetic diversity is greater in earlier stages of a GA then the genetic diversity should increase with increasing α . This implication was found to be true and is demonstrated by Figures A.6, A.12 and A.18. This added diversity was a goal of this thesis and can now be viewed as an accomplishment of this work.

The lack of increase in the average age of survivors displayed by Competition is also explainable. Consider that $\alpha_{ij} < 0$ implies that $c_{ij} < 0$. This means that there is no increasing expressed fitness as displayed by the other forms of co-evolution (the possible exception being just after the birth of the population). This implies that the average age of survivors is likely to be similar to the Regular GA, which it is.

It was hypothesized that the added genetic diversity provided by the co-evolutionary systems would permit a co-evolutionary GA to achieve better results than a regular GA. This hypothesis was found to be true and is demonstrated in Figures A.4, A.10 and A.16. However, there are some comments that should be made about the conditions under which the co-evolutionary GA attains higher absolute fitnesses are obtained.

Obviously competition for these three problems was largely ineffectual. Lower absolute fitnesses were recorded than the regular GA and there is little added genetic diversity. This does not say that competition should be excluded from co-evolutionary GAs however, competition without any other form of co-evolution

seems pointless.

For the other forms of co-evolution the optimization results varied depending on the problem. For Rosenbrock's function all three performed equally well, displaying similar behaviour. In almost all cases of α the co-co-evolutionary GA achieved better results than the regular GA. The typical behaviour displayed was that the co-evolutionary GA matched the fitness of the regular GA until the point where the regular GA converges. At about this point the co-evolutionary GA freezes¹¹ the set of survivors. Improvement in the fitness is then gained by the constant reproduction of the population (an example of this behaviour is shown in Figures A.1, A.2 and A.3).

While optimizing Griewangk's function and the Royal Road a wider range of results is obtained. It is clear from Figures A.6, A.12 and A.18 that the range of diversity obtained in Griewangk's function and the Royal Road function are higher than that obtained in Rosenbrock's function. As a result of this diversity the variation of fitnesses obtained is also large.

For high values of α the co-evolutionary GA freezes the survivors at an early generation. While this gains added diversity in the survivors it means a lower absolute fitness. In contrast, the low values of alpha converge readily keeping few older (and less fit on the absolute scale) individuals. When the survivors are finally frozen, little diversity remains and the GA is unable to improve further. It is in the compromise that the best results are obtained. The range of behaviours for Griewangk's function and the Royal Road function is best shown in Figures A.7, A.8, A.9, A.13, A.14 and A.15.

Traveling Salesman Problem The TSPs that were optimized here gave different results than the previous problems. However, the results obtained here indicate some of the limitations of co-evolutionary GAs. All three of the TSPs showed the same behaviour and hence it is unnecessary to describe all of the TSP problems in detail.

¹¹The term 'freezes' is used to denote the idea that the survivors are no longer changing.

Unlike the previous results, competition seemed to display an increase in the average age of the individuals. However, this was not due to the behaviour of the optimization but is a curiosity of the initial conditions described in Equation 4.8. Since $C_i(0) = f_i^a(0)$ this is the only source of change that might be negative. For the TSPs this initial change is always negative and in conjunction with negative connection weights promotes some individuals by giving them falsely inflated expressed fitnesses. This effect was seen only in the TSPs and could be removed by changing Equation 4.8 to reflect $C_i(0) = 0$. This was not deemed necessary as results in the TSP problem and competition were generally uninteresting.

The remainder of the forms of co-evolution did display an increase in the average age of surviving individuals. As in other problems this increase represents a resistance of older individuals to be removed from the surviving population. This variation was consistent with the other problems and as the α value increased the average age of survivors also increases (See Figures A.23, A.25 and A.27 for details).

Unfortunately, the behaviour of the regular GA is too poor for the co-evolutionary techniques to work. The regular GA has not yet converged to a specific path at 100 generations. Even extending the number of generations to 400 did not produce convergence (See Figure A.19). Since the regular GA has not yet converged the co-evolutionary GAs do not freeze their populations. This results in the co-evolutionary GA's resisting the input of new individuals into the surviving group to keep up genetic diversity. Yet without the new individuals the co-evolutionary GA does worst than the regular GA (See Figures A.22, A.24 and A.26 for details. Typical behaviour can be seen in Figures A.20 and A.21).

Chapter 7

Conclusions

7.1 Summary of Motivation and Goals

This thesis addresses the limited model that GAs and other forms of EC have previously used. This model is a simplistic model that has been examined for its range of behaviour and limitations. Based on a non-co-evolutionary approach to evolution the model allows for rapid convergence to a local optimum. Having found a local optimum the GA then proceeds to lose genetic diversity. This behaviour is counter to the intuitive behaviour of a biological system. This intuition states that populations should not lose diversity once they have converged to a stable state.

It is an assumption of this thesis that a prime reason for the loss of diversity is the lack of an accurate model. Of the various possible extensions to this model, the co-evolutionary approach seemed the most promising. The previous work in co-evolutionary GAs was a source of motivation. With this previous work in mind, the goals of this thesis were laid out in three specific sections:

- 1 Provide a coherent model of co-evolution representing as many possible forms of co-evolution as possible. The model should be fitness based with discrete time to be compatible with GAs.
- 2 This co-evolutionary model should provide the GA with genetic diversity in its populations. It should also be capable of producing better solutions to the problems being optimized.

- 3 The model should be as general as possible, having no dependence on GAs. It should offer mathematical precision and be consistent with previous definitions.

7.2 Contributions

The main contribution of this thesis is the successful completion of the goals set for this work. The remainder of contributions were made as a consequence of fulfilling these goals. All of these contributions are considered in the order that they appeared in this thesis.

The first accomplishment of this work is to compile a survey of the previous work in co-evolutionary techniques in GAs. This survey (presented in Chapter 2) represents the largest survey on the material to date. No previous surveys, known to the author, have focused on GA's nor have they presented the full spectrum of co-evolutionary implementations.

The definitions of Chapter 3 represent another significant contribution of this thesis. These definitions are based on the works of biology and are consistent with the previous work mentioned above. As such they represent the only proposed terminology that can be adhered to within the field of GAs. Previous work tried to convey the meaning with common usage and was often ambiguous. The definitions given here will avoid previous confusing descriptions while still allowing a full range of expression.

The next accomplishment attained by this work is the introduction of symbiosis graphs. In combination with the definitions of co-evolution, the symbiosis graphs represent a powerful graphical technique capable of representing complex relationships within a population. This was a necessary contribution because no well defined technique existed to accurately describe the individual relationships involved in the models presented here.

The introduction of the Symbiosis Model of Co-evolution represents a contribution to the field of fitness based co-evolutionary study. This model is unique in its

exact and flexible description of fitness relationships between individuals. Purposefully designed to be a mathematical framework for the study of co-evolution, it is also unique among the previous models as an extension of EC and GAs. Furthermore the mathematical definition of a linear connection and the presentation of the Linear Model of Symbiosis provides the necessary definition for the implementation of a GA or EC extension. It is not assumed nor was it shown that this extension changes the computational complexity of the GA. Co-evolutionary GAs are still Markov processes. The most probable absorbing states of the co-evolutionary GA are different from the regular GA but there is no indication that the computational power of the GA is altered.

Finally the implementation of the linear model represents the single largest contribution of this thesis. The results of the implementation clearly show a system that is self-governing which converges to local optima and yet preserves genetic diversity. In a large number of problems the implementation also shows an improvement over the regular GA. The magnitude of this improvement, in best fitness, is not always large. While the population in a co-evolutionary GA has a significant amount of genetic diversity it does not seem to translate to significant improvement in fitness. This raises the question of the worth of maintaining the genetic diversity. There are two motivations that validate this work. First the self-governing aspect of the system has undeniable benefits. For any problem the system will maintain a genetically diverse population. Secondly the added genetic diversity should allow GAs to optimize dynamic and noisy fitness functions. Unfortunately this was not in the initial scope of this thesis but is none the less important future work.

7.3 Future Work

The bulk of this work represents a step into the realm of co-evolution. As with all first steps there are many steps that must follow. The full scope of future work is tremendous, as large as the work previously done in GAs. The following section tries to illuminate some of the ideas that still need to be explored.

This preliminary experimentation with co-evolution shows that there are a number of measurements that might prove interesting in future analysis. first among these measurements is the number of pairs that survive together in Mutualism, Competition and Predation. Also the total effect of all individuals and the number of individuals effected would be interesting in less organized forms of co-evolution.

On the TSP problem a different crossover operator might prove more rewarding to co-evolution. The use of edge recombination is known to produce faster convergence in the regular GA [63] and is hypothesized as a solution to co-evolution's poor performance. It may also be possible to use heuristics on all new individuals¹. This would improve results and could encourage faster convergence in the regular GA. Since the co-evolutionary GA maintains diversity there is no need for the regular GA operators to be concerned with it.

Another interesting experiment would be to optimize the NK fitness landscape. By varying the ruggedness of the landscape the behaviour of co-evolution could be monitored and any correlations observed. This would clarify if the difference in behaviour between Rosenbrock's function and Griewangk's function is due to the ruggedness of the landscape.

Obviously not all the forms of linear co-evolution have been explored. The effects of different symbiosis forests in a population and across multiple populations have not been dealt with. Can simultaneously solving two problems aid in the quality of solutions for either or both? Can the breakup of a population into multiple populations aid in the quality of solutions obtained? Can the combination of different forms of symbiosis create behaviours not yet explored? Will the forms of co-evolution not involving feedback prove to be as rewarding as the forms with feedback (i.e., amensalism and commensalism). Would adaptism with a negative connection weight be beneficial? All of these questions will remain unanswered until sufficient research has been performed.

Further research is also possible by examining the effect of varying GA parameters, especially the replacement rate. Given that some problems respond differently

¹Such heuristics as 2-opt and 3-opt would improve the absolute fitness of each individual.

to different strengths of connections how would different replacement rates change a system's behaviour? By varying the parameters of the GA it may also be possible to obtain large scale benefits in optimizations. The full scope of benefits will not be determined until the variations of parameters has been examined.

But beyond the obvious forms of future work are some different and intriguing possibilities. This work has shown the linear symbiosis model to be capable of sustaining genetic diversity. It would also be interesting to see how the linear model does against a varying fitness function (i.e., a varying absolute fitness). The hypothesis based on the results of this thesis would be that when an absolute fitness changes it would not necessarily force a change in the population. Only after the absolute fitness had changed enough would the population respond. Then the population would quickly adapt to the new absolute fitness, several individuals would establish themselves as survivors and not be dislocated until sufficient change in the absolute fitness causes them to be "unfit".

This hypothesis is interesting because it would be analogous to the behaviour postulated by punctuated equilibrium and the theories of Stephen Gould and Niles Eldredge. Periods of stagnation (unchanging survivors) would be followed by periods of rapid change (changing survivors). While this is an oversimplification of the topic and only a hypothesis it is definitely worth analysis and experimentation.

Also interesting is the measure of diversity proposed by Thomas S. Ray in [55]. Instead of measuring hamming distance Ray has an entropy measure which measures diversity in the population. This entropy measure is $\sum_i -p_i \log p_i$ where i is a genotype or a genotypic feature and p_i is proportion of the population with that genotype or feature. As a diversity measure this could further prove that co-evolutionary GAs do increase genetic diversity.

Even beyond these areas of research it is possible to do studies of dependency effects. Suppose one organism is in a parasitic symbiosis with another individual and that individual dies. It is reasonable that the surviving individual should die too. These types of dependencies are an intriguing area of research. Would change in the the host population's absolute fitness cause a change in the parasite population?

What is the nature of the change and how would changing the absolute fitness of the host population affect the parasite population? Can the Red Queen Hypothesis be synthesized in this system?

It is also possible to use the linear model as a malleable model, where the connections of an individual are inherited from the parents or they are intrinsic to the genome of the individual. By placing the connections in the genome of an individual it is possible to evolve the form of co-evolution. This would be similar to Bull and Fogarty's work on the simulation of endosymbiosis but while the form of co-evolution was being evolved problems would also be optimized. This optimization provides a measure of how "well" the system has adapted on its scale of absolute fitness.

Finally another interesting possibility lies in the construction of new types of connections that more accurately model the diversity of symbioses. The immune system connection described in Chapter 4 is just one such example. It could also be possible to create communal connections where the effect of the connection would be a percentage of the affecting individual's absolute fitness. Within a group then the connections could be constructed to maintain the expressed fitnesses as the average of all individuals in the group.

The above section does not represent the entire scope of possible work. However it does represent the ideas that came to the author while working on this thesis. It is hoped that research in this area will continue and that the ideas presented here will be helpful in the continuation of that research.

Appendix A

A.1 Logistic Growth Equation

The Logistic Growth Equation given by A.1 models the population sizes of S populations in co-evolution with each other. The relationships between populations is similar to the relationships between individuals in symbiosis (See Chapter 3). Adapting the definitions of connection (See Definition 3.3) to apply between populations and not individuals and as affecting population size rather than fitnesses allows the classification of an arbitrary system by the a_{ik} values.

$$\frac{dN_i(t)}{dt} = N_i(t)(r_i + \sum_{j=1}^S a_{ij}N_j(t)) \quad (\text{A.1})$$

This analysis begins by examining two cases i) $a_{ik} < 0$ and ii) $a_{ik} > 0$. The analysis of each case will follow a standard strategy and notation. The assumption will be made that initially the system is in equilibrium. At time $t=0$ the population size N_k will change (i.e., $\frac{dN_k(0)}{dt} > 0$ or $\frac{dN_k(0)}{dt} < 0$) and the subsequent change in N_i after an infinitesimal time step will be calculated. This change in N_i after an infinitesimal time step dt will be written $dN_i(dt)$.

Since the system is initially at equilibrium, except for population k , Equations A.2 and A.3 can be derived from the condition of equilibrium $\forall i | i \neq k \{ \frac{dN_i(0)}{dt} = 0 \}$ and the Lotka-Volterra Equation (A.1).

$$N_i(0)(r_i + \sum_{j=1}^n a_{ij}N_j(0)) = 0$$

$$\rightarrow r_i + \sum_{j=1}^n a_{ij} N_j(0) = 0 \quad (\text{A.2})$$

and

$$\begin{aligned} \forall i | i \neq k, \frac{dN_i(0)}{dt} &= 0 \\ \rightarrow \forall i | i \neq k, N_i(dt) &= N_i(0) \end{aligned} \quad (\text{A.3})$$

Using Equations 4.3, A.2 and A.3 yields the following:

$$\begin{aligned} \frac{dN_i(dt)}{dt} &= N_i(dt) \left(r_i + \sum_{j=1}^n a_{ij} N_j(dt) \right) \\ \frac{dN_i(dt)}{dt} &= N_i(0) \left(r_i + a_{ik} (N_k(dt) - N_k(0)) + \sum_{j=1}^n a_{ij} N_j(0) \right) \\ \frac{dN_i(dt)}{dt} &= N_i(0) a_{ik} (N_k(dt) - N_k(0)) + N_i(0) \left(r_i + \sum_{j=1}^n a_{ij} N_j(0) \right) \\ \frac{dN_i(dt)}{dt} &= N_i(0) a_{ik} (N_k(dt) - N_k(0)) + \frac{dN_i(0)}{dt} \\ \frac{dN_i(dt)}{dt} &= N_i(0) a_{ik} (N_k(dt) - N_k(0)) + 0 \\ \frac{dN_i(dt)}{dt} &= N_i(0) a_{ik} (N_k(dt) - N_k(0)) \end{aligned} \quad (\text{A.4})$$

Now the two cases can be considered

Case i) $a_{ik} > 0$

Given $\frac{dN_k(0)}{dt} > 0$ then $N_k(dt) - N_k(0) > 0$ and by Equation A.4 $\frac{dN_i(dt)}{dt} > 0$.

Given $\frac{dN_k(0)}{dt} < 0$ then $N_k(dt) - N_k(0) < 0$ and by Equation A.4 $\frac{dN_i(dt)}{dt} < 0$.

Since a positive change in N_k results in a positive change in N_i and a negative change in N_k results in a negative change in N_i then $a_{ik} > 0$ corresponds to the connection: k protagonizes i ($k \xrightarrow{+} i$).

Case ii) $a_{ik} < 0$

Given $\frac{dN_k(0)}{dt} > 0$ then $N_k(dt) - N_k(0) > 0$ and by Equation A.4 $\frac{dN_i(dt)}{dt} < 0$.

Given $\frac{dN_k(0)}{dt} < 0$ then $N_k(dt) - N_k(0) < 0$ and by Equation A.4 $\frac{dN_i(dt)}{dt} > 0$.

Since a positive change in N_k results in a negative change in N_i and a negative change in N_k results in a positive change in N_i then $a_{ik} > 0$ corresponds to the connection: k antagonizes i ($k \bar{-} i$).

Using the knowledge that individuals

A.2 Evolutionary Game Theory and Stable Strategies

The Hawk and Dove game presented in Section 4.1.2 has exactly one ESS. The value of this ESS can be obtained from the previous definition of the problem and three subsequent definitions¹. Let p = the frequency of H strategists (i.e., Hawks) in the population. W_0 = the fitness of all individuals before competition and $W(H)$, $W(D)$ = the expected fitness of H (Hawk) and D (Dove) strategies respectively.

Then from [40] the expected fitnesses of a Hawk or Dove in a population is given by Equations A.5.

$$\begin{aligned} W(H) &= W_0 + pE(H, H) + (1 - p)E(H, D) \\ W(D) &= W_0 + pE(D, H) + (1 - p)E(D, D) \end{aligned} \quad (\text{A.5})$$

The population will remain at a specific ratio of Hawks to Doves (i.e., p will remain constant) if and only if the Hawks and Doves reproduce at the same rate (i.e., $W(H) = W(D)$). If $W(H) > W(D)$ then it is expected that more Hawks will be produced than Doves and p will increase. Conversely if $W(H) < W(D)$ then p will decrease. First the conditions under which p decreases will be dealt with.

¹ The following analysis is adapted from [40].

Given $W(H) < W(D)$ and substituting the expected fitnesses into Equations A.5 gives Equations A.6.

$$\begin{aligned}
 W(H) &< W(D) \\
 W_0 + pE(H, H) + (1 - p)E(H, D) &< W_0 + pE(D, H) + (1 - p)E(D, D) \\
 W_0 + \frac{p}{2}(V - C) + (1 - p)V &< W_0 + 0 + (1 - p)\frac{V}{2} \\
 V - pC &< 0 \\
 \frac{V}{C} &< p \\
 p &> \frac{V}{C}
 \end{aligned} \tag{A.6}$$

Thus p decreases when $p > \frac{V}{C}$. Similarly p increases when $p < \frac{V}{C}$ and p remains constant when $p = \frac{V}{C}$. Viewed from a strictly mathematical perspective it seems possible that p will approach $\frac{V}{C}$ whatever the initial condition and stay there. There is only one problem, not included in this analysis. The value of p always starts out between 0 and 1 and can never climb higher than 1. Using these constraints, it is clear that $p = \min(1, \frac{V}{C})$ is the only ESS of this system.

A.3 Results

The following pages of Tables and Figures represent the yet unspecified parameters and results. While this is not a comprehensive set of all results obtained it does summarize that which was obtained. For all graphs, each point is the average of 200 experiments. For analysis of performance it is also important to remember that the regular GA is equivalent to $\alpha = 0$. See Chapter 5 for descriptions of the implementation used, experimental parameters and results obtained.

Problem	Form of Co-Evolution	α
Rosenbrock	All	{0.0125, 0.025, 0.05, 0.075, 0.10, 0.135, 0.15, 0.165, 0.2, 0.25, 0.30, 0.35, 0.40,, 0.45, 0.50, 0.55, 0.60, 0.65, 0.7, 0.75, 0.80}
Griewangk	Adaptism	{0.0125, 0.025, 0.05, 0.075, 0.10, 0.15, 0.2, 0.25, 0.30, 0.35, 0.40, 0.45, 0.50, 0.55, 0.60, 0.65, 0.7, 0.75, 0.80}
	Mutualism	{0.0125, 0.025, 0.05, 0.075, 0.10, 0.15, 0.2, 0.25, 0.30, 0.35, 0.40, 0.45, 0.50, 0.55, 0.60, 0.65, 0.7, 0.75, 0.80}
	Predation	{0.0125, 0.025, 0.05, 0.075, 0.10, 0.15, 0.2, 0.25, 0.30, 0.35, 0.40, 0.45, 0.50, 0.55, 0.60, 0.65, 0.7, 0.75, 0.80}
	Competition	{0.0125, 0.025, 0.05, 0.075, 0.10, 0.20, 0.40, 0.80}
Royal Road	Adaptism	{0.0125, 0.025, 0.05, 0.10, 0.15, 0.2, 0.25, 0.30, 0.35, 0.40, 0.45, 0.50, 0.55, 0.60, 0.65, 0.7, 0.75, 0.80}
	Mutualism	{0.0125, 0.025, 0.05, 0.10, 0.15, 0.2, 0.25, 0.30, 0.35, 0.40, 0.45, 0.50, 0.55, 0.60, 0.65, 0.7, 0.75, 0.80}
	Predation	{0.0125, 0.025, 0.05, 0.10, 0.15, 0.2, 0.25, 0.30, 0.35, 0.40, 0.45, 0.50, 0.55, 0.60, 0.65, 0.7, 0.75, 0.80}
	Competition	{0.05, 0.10, 0.20, 0.40, 0.80}
TSPs	All	{0.05, 0.10, 0.15, 0.2, 0.25, 0.30, 0.35, 0.40, 0.45, 0.50, 0.55, 0.60, 0.65, 0.7, 0.75, 0.80}

Table A.1: These are the strengths of connections used during experimentation.

Figure A.1: This graph shows the best absolute fitness ever achieved by Adaptism while optimizing Rosenbrock's Function (the maximum possible fitness is 0). Clearly both extremes of α perform better than the regular GA. It is important to note that the co-evolutionary GAs continue to improve while the regular GA converges to a local optimum. For details on performance across α see Figure A.4.

Figure A.2: This graph shows the average age of survivors achieved by Adaptism while optimizing Rosenbrock's Function. The trend demonstrated in this graph is that with higher values of α the average age of survivors increases (i.e., the survivors stop being replaced at earlier generations with higher α). For details on performance across α see Figure A.5.

Figure A.3: This graph shows the average Hamming distance from the survivors to the current best survivor achieved by Adaptism while optimizing Rosenbrock's Function (the binary string length was 32 bits). For this problem even the weakest connection weight causes a dramatic increase in genetic diversity. Also important is the fact that genetic diversity plateaus very early (7th to 20th generation) and never decreases further. For details on performance across α see Figure A.6.

Figure A.4: This graph shows the best absolute fitness achieved before the 100th generation. The function being optimized is Rosenbrock's Function and the maximum possible fitness is 0.

Figure A.5: This graph shows the average age of survivors at the 100th generation while optimizing Rosenbrock's Function.

Figure A.6: This graph shows the average Hamming distance from survivors to the current best survivor to at the 100th generation while optimizing Rosenbrock's Function. The binary string length was 32 bits.

Figure A.7: This graph shows the best absolute fitness achieved by Predation while optimizing Griewangk's Function (the maximum possible fitness is 0). The curve for $\alpha = 0.8000$ demonstrates a freezing of the survivors too early. Despite a lot of diversity it is unable to outperform the regular GA. The curve for $\alpha = 0.0125$ demonstrates a freezing of the population too late. Despite converging to a high fitness level the lack of genetic diversity once the survivors do freeze restricts the overall performance of the co-evolutionary GA. Finally $\alpha = 0.0750$ is the compromise that outperforms all others tested. For details on performance across α see Figure A.10.

Figure A.8: This graph shows the average age of survivors achieved by Adaptism while optimizing Griewangk's Function. Clearly a higher value of α corresponds to a higher average age of survivors. For details on performance across α see Figure A.11.

Figure A.9: This graph shows the average Hamming distance from survivors to the current best survivor achieved by Predation while optimizing Griewangk's Function (the binary string length is 32 bits). For this problem there is a wide range of increase in genetic diversity with varying α . Also important is the fact that once genetic diversity plateaus in the co-evolutionary GA it never decreases further. For details on performance across α see Figure A.12.

Figure A.10: This graph shows the Best Absolute Fitness achieved by the 100th generation. The function being optimized is Griewangk's Function and the maximum possible fitness is 0.

Figure A.11: This graph shows the Average Age of Survivors at the 100th generation while optimizing Griewangk's Function.

Figure A.12: This graph shows the average Hamming Distance from survivors to the current best survivor to at the 100th generation while optimizing Griewangk's Function. The binary string length was 32 bits.

Figure A.13: This graph shows the best absolute fitness achieved by Adaptism while optimizing Holland's Royal Road Function (the maximum possible fitness is 12.8). The curve for $\alpha = 0.80$ demonstrates a freezing of the survivors too early. Despite a lot of diversity it is unable to outperform the regular GA. The curve for $\alpha = 0.05$ demonstrates a freezing of the population too late. Despite converging to a high fitness level the lack of genetic diversity once the survivors do freeze restricts the overall performance of the co-evolutionary GA. Finally $\alpha = 0.4$ is the compromise that outperforms all others shown. For details on performance across α see Figure A.16.

Figure A.14: This graph shows the average age of survivors achieved by Adaptism while optimizing Holland's Royal Road Function. For details on performance across α see Figure A.17.

Figure A.15: This graph shows the average Hamming distance from survivors to the current best survivor achieved by Adaptism while optimizing Holland's Royal Road Function (binary string length is 240 bits). For this problem there is a wide range of increase in genetic diversity with varying α . Also important is the fact that once genetic diversity plateaus in the co-evolutionary GA it never decreases further. The $\alpha = 0.40$ curve does not plateau because, as Figure A.14 indicates, by the 100th generation it does not have a frozen set of survivors. For details on performance across α see Figure A.18.

Figure A.16: This graph shows the best absolute fitness achieved by the 100th generation. The function being optimized is Holland's Royal Road Function and the maximum possible fitness is 12.8.

Figure A.17: This graph shows the average age of survivors at the 100th generation while optimizing Holland's Royal Road Function.

Figure A.18: This graph shows the average Hamming distance from survivors to the current best survivor to at the 100th generation while optimizing Holland's Royal Road Function. The binary string length was 240 bits.

Figure A.19: This graph shows the best fitness ever achieved by the regular GA on a 51 City TSP (EIL51). The maximum possible fitness is -426. This graph is important because it shows that despite only having 100 individuals in the population the regular GA has not converged after 400 generations.

Figure A.20: This graph shows the best fitness ever achieved on a 51 City TSP (EIL51) by Adaptism (the maximum possible fitness is -426). For details on performance across α see Figure A.22.

Figure A.21: This graph shows the average age of survivors achieved on a 51 City TSP (EIL51) by Adaptism. This behaviour of increasing average age with increasing α is consistent with the other problems. Missing is the freezing of the populations as demonstrated in Figure A.15 by the upturn in slope. It is hypothesized that this did not occur in this problem because the regular GA did not converge to a local optima. For details on performance across α see Figure A.23.

Figure A.22: This graph shows the best absolute fitness achieved by the 100th generation. The function being optimized is 51 City TSP (EIL51) and the maximum possible fitness is -426.

Figure A.23: This graph shows the average age of survivors at the 100th generation while optimizing a 51 city TSP (EIL51).

Figure A.24: This graph shows the best absolute fitness achieved by the 100th generation. The function being optimized is 76 City TSP (EIL76) and the maximum possible fitness is -538.

Figure A.25: This graph shows the average age of survivors at the 100th generation while optimizing a 76 city TSP (EIL76).

Figure A.26: This graph shows the best absolute fitness achieved by the 100th generation. The function being optimized is 101 City TSP (EIL101) and the maximum possible fitness is -629.

Figure A.27: This graph shows the average age of survivors at the 100th generation while optimizing a 101 city TSP (EIL101).

Appendix B

Glossary

Amensalism *Amensalism* occurs between two individuals *Host* and *Amensal* if and only if $Host \dashv Amensal$ such that *Amensal* does not affect the fitness of *Host*.

Antagonist Connection The relationship $A \rightarrow B$ between individuals *A* and *B* is defined to be an *antagonist connection* $A \dashv B$ (read: *A* antagonizes *B*) if and only if there exists a connection $A \rightarrow B$ such that as the fitness of *A* decreases, the fitness of *B* increases and as the fitness of *A* increases the fitness of *B* decreases.

Absolute Fitness The *absolute fitness* of individual x_i at time t , $f_i^a(t)$, is defined to be the individual's fitness without any effects by other individuals. Thus absolute fitness $f_i^a(t)$ is dependent on the genotype and phenotype of x_i , the environment and time t (for a definition of environment see Definition 1.5).

Adaptism Given one individual, *Adaptism* occurs if and only if $Individual \dashv Individual$ or $Individual \dashv Individual$.

Co-evolution *Co-evolution* of a population with itself occurs when individuals within the population are in symbiosis with other individuals in the same population. *Co-evolution* of a pair of populations with each other occurs when individuals in one population are in symbiosis with individuals of the other population.

Commensalism *Commensalism* occurs between two individuals *Host* and *Commensal* if and only if $Host \perp^+ Commensal$ such that *Commensal* does not affect the fitness of *Host*.

Competition *Competition* occurs between two individuals *Competitor A* and *Competitor B* if and only if $Competitor A \vdash Competitor B$ and $Competitor B \vdash Competitor A$.

Connection Given that there is a symbiosis between two individuals *A* and *B*, a *connection* (denoted: $A \rightarrow B$, read: *A* affects *B*) exists if and only if the fitness of *A* has a direct affect on the fitness of *B*.

Environment An individual's *Environment* is the collection of all fitness factors of the individual that are not individuals.

Expressed Fitness The *expressed fitness* of individual x_i at time t , $f_i^e(t)$, is defined to be the individual's fitness including the effects of all individuals. The expressed fitness is therefore dependent on the genotype and phenotype of x_i , the environment, time t and all individuals x_j such that $x_j \rightarrow x_i$.

Fitness Factor A *Fitness Factor*, of an individual, is anything which, when altered, can produce a change in the fitness of an individual.

Indirect Antagonist Connection An *indirect antagonist connection* $A \hat{=} B$ (read: *A* indirectly antagonizes *B*) is said to exist between individuals *A* and *B* if and only if the fitness of *A* indirectly affects the fitness of *B* and when the fitness of *A* increases the fitness of *B* decreases and when the fitness of *A* decreases the fitness of *B* increases.

Indirect Protagonist Connection An *indirect protagonist connection* $A \hat{=} B$ (read: *A* indirectly protagonizes *B*) is said to exist between individuals *A* and *B* if and only if the fitness of *A* indirectly affects the fitness of *B* and when the fitness of *A* increases the fitness of *B* increases and when the fitness of *A* decreases the fitness of *B* decreases.

Mutualism *Mutualism* occurs between two individuals *SymbiontA* and *SymbiontB* if and only if $SymbiontA \stackrel{+}{\sim} SymbiontB$ and $SymbiontB \stackrel{+}{\sim} SymbiontA$.

Predation *Predation* occurs between two individuals *Predator* and *Prey* if and only if $Predator \stackrel{-}{\sim} Prey$ and $Prey \stackrel{+}{\sim} Predator$.

Protagonist Connection The relationship $A \rightarrow B$ between individuals *A* and *B* is defined to be a *protagonist connection* $A \stackrel{+}{\sim} B$ (read: *A* protagonizes *B*) if and only if there exists a connection $A \rightarrow B$ such that as the fitness of *A* increases, the fitness of *B* increases and as the fitness of *A* decreases the fitness of *B* decreases.

Reproductive Fitness An individual's *Reproductive Fitness*, at time *t*, is the probability that the individual will reproduce before time $t + 1$.¹

Survival Fitness An individual's *Survival Fitness*, at time *t*, is the probability that the individual will survive until time $t + 1$.

Symbiosis *Symbiosis* is defined by a relationship between two individuals where the fitness of one individual directly affects the fitness of the other individual.

¹It is assumed here that "reproduce" means that offspring will be born between times *t* and $t + 1$.

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IMAGE EVALUATION TEST TARGET (QA-3)

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