AN AXIOMATIC DEVELOPMENT

OF

THE IDEAS UNDERLYING DARWINIAN NATURAL SELECTION

by

Mary Bearden Williams

A thesis submitted for the degree of Doctor of
Philosophy of the University of London

July 1967.

Imperial College of Science and Technology,
London, S.W.7.

ABSTRACT

In this thesis a set of axioms sufficient to generate the Darwinian theory of natural selection is developed and some of the implications of the theory derived.

In the process of developing the axioms the basic assumptions of the theory are clarified and the doubts raised by its apparent tautological nature resolved.

The theorems derived from the axioms show that certain consequences that must be derivable in a theory of natural selection can be derived. (E.g. One theorem shows that there is always a subpopulation, fitter than the population as a whole, which is in the process of taking over the population; other theorems show that under certain circumstances less fit subpopulations will be eliminated.) They also show that the axiomatized theory has various expected consequences. (E.g. One theorem states consequences of density dependent selective advantage; several theorems show differences between natural selection in interbreeding populations and natural selection in non-interbreeding populations.) Thus the theorems provide evidence for the assertion that these axioms will generate the Darwinian theory of natural selection.

Two further axioms are stated in order to indicate how the axiomatized theory of natural selection can be embedded within an axiomatized theory of evolution and further theorems are proved with the use of these axioms.

ACKNOWLEDGEMENTS

I should like to thank Professor Dennis Gabor, F.R.S. for acting as my supervisor, Mr. Jack D. Cowan for advice and guidance to the literature, and the National Institute of General Medical Sciences of the United States Public Health Service for financial support (Fellowship number: 2-F1-GM-23, 899).

CONTENTS

CHAPTER 1 : HISTORICAL INTRODUCTION

Section 1.1: Darwin's Theory of Natural Selection

To the layman, Darwin's claim to greatness lies in his theory of evolution; to the biologist, it lies in his theory of natural selection. This theory was well summarised by Darwin in the following paragraph from The Origin of Species:(1)

> "If under changing conditions of life organic beings present individual differents in almost every part of their structure, and this cannot be disputed; if there be, owing to their geometrical rate of increase, a severe struggle for life at some age, season, or year, and this certainly cannot be disputed; then, considering the infinite complexity of the relations of all organic beings to each other and to their conditions of life, causing an infinite diversity in structure, constitution, and habits, to be advantageous to them, it would be a most extraordinary fact if no variations had ever occurred useful to each being's own welfarw, in the same manner as so many variations have occurred useful to man. But if variations useful to any organic being ever do occur, assuredly individuals thus characterized will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance, these will tend to produce offspring similarly characterised. This principle of preservation, or the survival of the fittest, I have called Natural Selection."

Succeeding generations of biologists have filled in the details of "the strong principle of inheritance" and of the nature of the occurrence of variations, but Darwin's principle of natural selection is, essentially unaltered, the basis of the modern theory of evolution.

Section 1.2: The Modification of Species over Time

By his massive presentation of the evidence for evolution, Darwin convinced the world that evolution had in fact occurred, but with the emergence of an understanding of the mechanism of heredity (i.e. Mendelian genetics) the efficacy of Darwinian selection as a force in evolution began to be seriously questioned, for selection appeared to be a weak force compared to the power of mutation, and a propensity for single factor theories of evolution hindered the recognition that a combination of mutation and natural selection was necessary. According to Huxley:(2)

> "It was not until about 1930 that the facts behind the chromosome theory and the mutation theory could be finally reconciled with the idea of gradual evolutionary change and the selective origin of adaptations in what R.A. Fisher called, in the title of his important book 'The Genetical Theory of Natural Selection'."

(It is important to note that Fisher's work was a reconciliation of genetics and natural selection, not a derivation of natural selection from genetics.) Largely as a result of Fisher's work:(3)

> "The many dissenting theories were almost suddenly fused, in the 1930's, into a broad unified theory, the 'synthetic theory'....In essence it is a two factor theory, considering the diversity and harmonious adaptation of the organic world as the result of a steady production of variation and of the selective effects of the environment".

Thus, by the 1930's, the concepts of mutation, gene, and population had been added to the theory of evolution, clarifying the mechanisms of variance and inheritance and elucidating the role of natural selection. This essentially completed the theory of the modification of species over time, though many details still remain to be clarified.

Section 1.3: The Origin of Species

This understanding of the modification of species did not, however, provide an understanding of the origin of species (i.e. the splitting of one species into two species). As Mayr comments:(4)

> "It was not possible to state the problem of the multiplication of species with precision until the biological species concept had been developed."

The essential prerequisite for the development of the biological species concept was provided by Dobzhansky in 1940 in his paper introducing the idea of isolating mechanisms;(5) over the next twenty years this idea was explored and developed by Dobzhansky, Mayr,(6) and others, resulting in the statement of the biological species concept, which defines species as sets of organisms which interbreed within their own set and are reproductively isolated from organisms in other sets. Once the species has been defined in these terms it is possible to ask how species split by asking how reproductive isolation can develop between organisms within a set. It is also possible to ask what the role of natural selection may be in maintaining fertility between organisms in the same set and reducing fertility between organisms from the two parts of a splitting set. Answers to these questions have been put forth by the proponents of the biological species concept, but they have not coalesced into a really definitive theory. These concepts are, however, expected to form the basis of a definitive explanation of the origin of species.

Section 1.4: On the Relation Between Natural Selection and Evolution

Notice that the two previous sections have not discussed the history of the development of the theory of natural selection; they have discussed the history of the development of the application of the theory to the theory of evolution. Natural selection is a part of the theory of evolution but the theory of evolution is not a part of it. Thus the theory of evolution has been presented here not because it can be derived from the theory of natural selection but because it provides a practical background against which the theory (and hence the axiomatization of the theory) can be judged; this fact has been used extensively in the development of this axiomatization to discover in the early statements of the axioms, errors which would lead to obviously false statements in the theory of evolution. The reader may similarly use the theory of evolution to test the final statements of the axioms.

Section 1.5: Mathematical Approaches

Because of the enormous number of generations involved in modification through natural selection, particular consequences of its action are not easily understood by the intuitive methods which form the basis of most biological thinking. Intuition is necessarily based on experience with a relatively few generations and, because of the non-deterministic nature of the individual events, experience with them is not easily extrapolated by intuition alone to generalisations about the course of events over millions of years. Thus it is not surprising that the most important theoretical contribution of mathematics to biology has been in the field of evolution.

This contribution has been made by statistical genetics, which proved that Mendelian heredity and natural selection could work together to produce the characteristics of natural populations. It proved that effects which intuition had dismissed as negligible(7) could be most important in producing evolutionary change. It proved that effects, such as altruism,(8) which intuition had decided certainly could not be produced by natural selection, could be produced by natural selection. And, of course, it confirmed the possibility of many effects which intuition had decided would be produced by natural selection.

As yet, no other mathematical approach has made a comparable contribution to the understanding of evolution, though this is not because there are no further important problems. Two different approaches will be described below in order to provide further orientation in what has been done, mathematically, in this area and in order to mention some light which they incidentally throw on the relation between Mendelian genetics and natural selection.

J.H. Woodger has pioneered the application of the axiomatic method to biological problems,(9) using the techniques of Principia Mathematica(10) in an attempt to provide a logically solid foundation for genetics. (These techniques will be familiar to the mathematical reader; Woodger's axiomatization will not be discussed in detail here as the axiomatization presented in this thesis is independent of it.) This work, in addition to clarifying the foundations of genetics, has led to some clarification of the taxonomic problem of classifying groups of animals which are in the process of becoming distinct species; this taxonomic work has been done by Woodger himself(11) and by Gregg.(12) Woodger has further used these techniques in a recent paper on random (i.e. non-selective) evolution(13) thus underlining the fact that natural selection is not a necessary consequence of Mendelian genetics.

Still another mathematical approach to evolution has been developed by Barricelli,(14) whose principal technique is computer simulation. He studies the effects of certain artificial reproduction rules on patterns of numbers (called symbioorganisms) which are created, from a first generation of random numbers, by the repeated application of the rules. He claims to have obtained such phenomena as selection, competition, and even parasitism, though it is impossible to evaluate these claims without more of the computer output than has been published and, more important, without explicit definitions, acceptable to the whole biological community, of these terms. The apparent ability to obtain evolutionary phenomena in a selective but decidedly non-Mendelian universe is, however, interesting in underlining the fact that Mendelian genetics is not a necessary consequence of natural selection.

Section 1.6: Conclusion

This chapter has provided an orientation to the state of development of the theory of natural selection and of the related theories in terms of which it is usually discussed, namely the theories of evolution and of Mendelian genetics. It has further provided an orientation to the mathematical approaches which have been developed to elucidate these theories. It has not provided a history of the axiomatic development of the theory of natural selection because, to the author's knowledge, there is none.

CHAPTER 2 : INTRODUCTION

Section 2.1: Purpose

What are the basic assumptions of the theory of natural selection? What are their implications? It is the purpose of this thesis to attempt to answer these questions, particularly the first. The axioms that will be stated, are, we assert, an explicit statement of the basic assumptions of the theory of natural selection. The theorems that will be stated are a few of the implications of these assumptions.

The reasons for this attempt are twofold: firstly because the lack of an explicit statement of the theory has led to serious question of its worth; and secondly because the great difficulty of deriving in a human lifetime an intuitive understanding of a process occurring over millenia points to a need for a mathematical tool to aid the intuition. The goal implied by the first reason is achieved in the thesis; the serious charge of tautological reasoning is answered. The goal implied by the second reason is achieved to some at present unknowable extent; the only way to prove the achievement of this goal is to show a statement derivable from the axioms which is important, not intuitively predictable, and either intuitively or verifiably true; no such theorem has yet been derived (though important, intuitively predictable ones have been), but this is hardly surprising at this stage of the development of the system. Thus the axiom system achieves the first goal and gives some reason to believe that it may achieve the second.

Section 2.2: Two Concepts Which Are not Essential to the Theory

It has, since Fisher published The Genetical Theory of Natural Selection, been usual to regard natural selection as almost a part of Mendelian heredity; natural selection is almost never considered independently of Mendelian heredity. However, as was mentioned in the previous chapter, natural selection is independent of Mendelian heredity; this is not surprising since Darwin derived the theory while believing in an antithetical mechanism of inheritance. Therefore it is a part of the task of this thesis to separate the theory of natural selection from the genetical theory of natural selection. By so doing we shall clarify not only the process of natural selection but also the extent to which different theories of heredity are compatible with it.

Just as we shall ignore, without denying, the Mendelian mechanism of heredity, so also we shall ignore, without denying, the statistical aspect of the details of the process of natural selection. Newton has shown in physics that it is possible to describe, without statistics, the global behaviour of a system in which every individual event is determined not by deterministic laws but only by statistical laws. Similarly Darwin has shown (though not as precisely) in biology that it is possible to describe, without statistics, the global behaviour of a system in which every individual event is determined not by deterministic laws but only by statistical laws. Newton's success in ignoring statistics is based on the fact that the size of the objects considered is so large that the statistical behaviour is smoothed into average behaviour. Darwin's success in ignoring statistics is based on the fact that the size of the time interval considered is so large that the statistical behaviour is smoothed into average behaviour. Thus there is considerable historical evidence to support the contention that a theory may be very useful, even though it ignores the statistical aspects of the phenomena, as long as the numbers involved in the phenomena are large enough. By taking advantage of this historical precedent and ignoring the statistical aspects, we shall be able to present the theory in its simpler form.

There is yet another concept which might be expected to play an important part in the axiomatization which we shall ignore. This, unlike, the previous, biological concepts, is a technical mathematical concept and will be best mentioned within the context of a description of the axiomatic method; since such a description is in any case necessary to orient the non-mathematical reader, it will be presented in the following section.

Section 2.3: The Axiomatic Method

The axiomatic method begins by setting forth certain fundamental statements, the axioms, which the reader is asked to accept, without proof, as the basic assumptions of the theory; thus "If L is a line then there exists a point not on L." is one of the axioms of Euclidean geometry, while the law of the survival of the fittest is one of the axioms of the theory of natural selection. Axioms are usually intuitively reasonable statements about the concept which is to be axiomatised; thus the two examples cited above are intuitively reasonable statements about, respectively geometry and natural selection. From these axioms it will be possible, using the methods of proof made familiar by Euclidean geometry, to deduce other statements, the theorems, which therefore must be true if the axioms are true; thus "Every point is on at least two distinct lines." is one of the theorems of Euclidean geometry, while "No organism is its own ancestor." is one of the theorems of natural selection. The theorems themselves provide a check on the truth of the axioms, for if a theorem which is demonstrably not true of the concept which was axiomatized is derivable from the axioms, then at least one of the axioms is not true; this means that the discovery of an error in an axiomatized theory necessitates correction of the error at its source (possibly in the basic structure of the theory) which prevents the unlimited proliferation of *ad hoc* assumptions which makes much of biology resemble a patchwork quilt. Hence the axiomatic method allows the number of statements which have to be accepted solely on the grounds of intuitive probability to be reduced to a bare minimum, and it provides a check on the truth of those that are accepted on such grounds.

These axioms contain certain words, the undefined terms, which usually have a relatively clear intuitive meaning but whose meaning is never explicitly stated; thus "point" and "line" are undefined terms in Euclidean geometry, while "fitness" and "organism" are undefined terms in the theory of natural selection. These terms, though undefined, are not completely free from restriction on their meaning, for they are limited by the assumption that the axioms are true statements about them; thus "organism" may be thought of as meaning "bacterium", "plant", or any of many other possibilities, but it may not be thought of as meaning, e.g., "real number", for a real number does not have ancestors with the properties stipulated in the axioms. Just as all other statements in the theory are proved by using the axioms together with the laws of logic, so all other terms in the theory are defined by using the undefined terms together with the terms of logic.

These laws and terms of logic constitute the other concept which it was mentioned would be ignored. By this we mean not that we shall not use them (for we must) but that we shall not explicitly state them and that when we use them we shall not explicitly state that we are using them. This is possible because these laws are in large part derived from (and presumably form the basis of) our usual intuitive method of reasoning and hence we may assume that in using this method we shall not contravene the laws. This assumption may in some cases be false, but the simplification made possible by the assumption is great ehough, and the risk is small enough, that most mathematicians prefer to take the risk. We shall, therefore, use the methods of reasoning commonly used by mathematicians rather than the formal methods of mathematical logic.

Section 2.4: Description of the System - Introduction

We shall separate the axioms into three sets, which shall be described briefly in this section and more fully in the following sections. The first set describes a system which we call a Biological Universe; this system is simply the biological background which Darwin, and everyone else, took for granted. The second set describes a system which we call a Darwinian Universe; this set describes the theory of natural selection and places it in the above mentioned biological background. The third set describes a system which we call a Diverse Darwinian Universe; this set adds to the concepts of the Darwinian Universe the concept of the existence of different environments.

Section 2.5: Description of the System - Biological Universe

The axioms of the Biological Universe are probably the only ones in the thesis which are simple enough to be called self-evident truths. They are the following very simple statements about the ancestor-descendant relation: no organism is its own parent; if organism_1 (read "organism sub one") is an ancestor of organism_2 then organism_2 is not an ancestor of organism_1; if organism_1 is equal to organism_2 then every ancestor of organism_1 is an ancestor of organism_2 (this is really a statement about what we mean by "is equal to"); there are a finite number of organisms in any one generation of any population. With these axioms we can prove several theorems which are useful later in proving theorems that are consequences of natural selection. But the main purpose of stating these axioms is simply to provide the background which is necessary in order to state the axioms of natural selection, for it is impossible to discuss either the successive generations of a population or inheritance without some statement of what is meant by "ancestor". Thus a Biological Universe is simply a set of organisms which are related to other organisms in the set by the ancestor relation.

Section 2.6: Description of the System - Darwinian Universe

The Darwinian Universe is described by the same number of axioms as the Biological Universe, but the axioms are much more complicated. The first states that the populations that will be the object of discussion satisfy the axioms of the Biological Universe. The second introduces the concept of the fitness of an organism, stipulating that the fitness can be described numerically. The third is the survival of the fittest axiom, which states that the universe is such that in the long run a fitter subpopulation will increase in numbers relative to a less fit subpopulation; the statement of this is necessarily rather complicated as the phrase "in the long run" covers a very complicated concept. The fourth is the hereditary variation axiom, which is also very complicated as we must state in it that fitness is hereditary but not too hereditary; i.e. that there are changes whose influence is sufficiently lasting to change the composition of the population but not sufficiently lasting to forbid further changes. Together these four axioms give the properties of the Darwinian Universe; it is a set of populations with a fitness assumed for the individual members of the populations which is such that (1) there are always some lineages that are fitter than others, and (2) the numbers of descendants in these lineages will increase relative to the numbers of descendants in the less fit lineages.

Section 2.7: Description of the System - Diverse Darwinian Universes

In the Darwinian Universe the concept of environment is never explicitly mentioned, though certain properties of the environment are implicitly described in the axioms. For example, since fitness is a property of an organism in an environment, the statement that fitness is reasonably hereditary implies that the environment is reasonably stable. Similarly the source of the new variation guaranteed by the hereditary variation axiom may be in change in the environment or it may be in change in the hereditary elements within the organism. Also, to give yet another example, the survival of the fittest axiom may be seen as a statement about the type of environment in which the organisms live. But, although these axioms do indicate some properties of the environment in their statement of the environment-organism relationship, they never indicate that a particular organism may have one fitness in one environment and quite another fitness in another environment; in fact the axioms do not allow this possibility since the fitness function assigns a unique fitness to each organism. Thus while the Darwinian Universe describes the modification of populations in the time dimension, it cannot account for the modification of one population into two populations by selective forces acting in opposite directions.

As is indicated in the previous chapter, this is not the result of a failure to completely translate Darwin's insights into explicit statements, for(15)

> "Darwin failed to solve the problem indicated by the title of his work. Although he demonstrated the modification of species in the time dimension, he never seriously attempted a rigorous analysis of the problem of the multiplication of species, of the splitting of one species into two."

Thus in order to describe the splitting of species it is necessary to go beyond the Darwinian Universe, to add axioms which formalize post-Darwinian insights. These post-Darwinian insights are not insights into the process of natural selection but rather into the way in which natural selection interacts with the diversity of environments to produce the diversity of species. To axiomatize these insights is clearly not a part of the stated task of the thesis; however it is very difficult to gain an intuitive understanding of the Darwinian Universe without some discussion of how it interacts with the diversity of environments, so we shall present a partial axiomatization of these post-Darwinian insights. This axiomatization will be neither complete nor definitive, but it will answer some of the questions about how the Darwinian Universe can be embedded into a larger universe in which the origin of species can be explained.

A Diverse Darwinian Universe is essentially a set of Darwinian Universes which have different fitness functions and therefore different selective properties. It is described by two axioms: the first states that each fitness function behaves as a fitness function in a Darwinian Universe; the second states that for each population there are at least two different fitness functions with opposite selective properties. With these axioms it is possible to work out some of the consequences of the existence of environments with different selective properties.

Section 2.8: Description of the Presentation

The substantive part of the thesis thus consists of three sets of axioms together with the statements and proofs of a few of the theorems which can be derived from them; these are found, for each Universe, in the appendix at the end of the relevant chapter. The majority of the thesis, however, is devoted to explaining (with biological examples in the most complicated cases) the meaning of the axioms, definitions, and theorems. There are no mathematical prerequisites for understanding them other than a vague grasp of the concept of function. (It must be admitted, though, that a real appreciation of the system would probably require not only what is called mathematical maturity but also its analog, biological maturity.) Thus, though a solid mathematical background and a solid biological background would be helpful, neither is required for understanding our answer to the questions stated at the beginning of this chapter. This answer is given in the following chapters.

CHAPTER 3 : BIOLOGICAL UNIVERSES

Section 3.1: Undefined Concepts

Before we can discuss natural selection we must delineate the objects upon which natural selection works. These objects are sets of organisms and their descendants. Thus the objects are themselves structured entities and it will be necessary to state this structure in axioms in order to provide a firm foundation for the later axiomatization of the process of natural selection.

The difficulty of defining "life" has been pointed out so often that it will come as no surprise to the reader that we shall take "organism" as an undefined concept. By "organism" we shall mean (intuitively) the same self-reproducing living entities that are the usual objects of study in biology. However, if there should happen to be other entities, not usually considered alive, which satisfy the axioms in this chapter, then they will, within this system, be considered to be perfectly respectable organisms. Similarly, if there should happen to be entities which are usually considered to be alive but which do not satisfy all of the axioms in this chapter, then these entities will not, within this system, be considered to be organisms. Thus, any entity which is part of a group which satisfies these axioms is an organism; any entity which is not contained within such a group is not an organism.

The reader should, therefore, while reading each axiom, decide if there are any entities which he would call organisms which do not satisfy the axiom and, after reading all of the axioms, decide whether there are any entities which he would not call organisms which satisfy the axioms. If there are any entities of the first kind, then he should note that nothing that we subsequently assert to be true of all organisms can be taken to be necessarily true of these entities. If there are any entities of the second kind, then he should note that our "definition" of organism is wider than his "definition" of organism. It is desirable that there be very few (if any) entities of the first kind; it is immaterial for our purposes whether there be few or many entities of the second kind. (In fact, for a given axiom system, the more different types of entities there are which satisfy the axioms, the more interesting is the system.) The axioms should characterize at least the vast majority of those entities which are normally considered to be organisms.

The other concept which will be defined only by the way in which it is used in the axioms is the concept of parent, or immediate ancestor. This concept is not of an entity but of a relation between entities. In this it is similar to, for example, the relation "greater than" used in arithmetic. Just as one says "five is greater than four", one also says "John is a parent of Jim". These two relations are also similar in having a direction: the statement "five is greater than four" is not the same as the statement "four is greater than five"; similarly the statement "John is a parent of Jim" is not the same as the statement "Jim is a parent of John". For the relation "is greater than" the symbol ">" is generally used; for the relation "is a parent of" the symbol "A>" will be used. Thus "John A> Jim" will be used to mean "John is a parent of Jim". This symbol is a combination of the letter "A" and the symbol for "is greater than"; the letter "A" appears closest to the ancestral (i.e. parent) organism and this fact can be used as a mnemonic device for remembering which is the parent organism. If necessary, the symbol may be reversed so that the name of the descendant comes first: thus "Jim <A John" also means "John is a parent of Jim" (or "Jim is an immediate descendant of John"); note that the letter "A" still appears closest to the organism which is the ancestor. We note also (as another mnemonic device) that the pointed end of the symbol points at the younger organism, the one whose age is "less than" the age of the other, just as the pointed end of the "is greater than" symbol in "5 > 4" points at the smaller number. It would, clearly, be ridiculous to use names like John and Jim for all of the organisms we will discuss; we shall hereafter, denote an organism by the letter "O" (for organism) with a subscript or superscript to allow us to distinguish between different organisms. Thus we shall use "$O_1 \mathrel{A\!\triangleright} O_2$" to mean "organism sub-one is the parent of organism-sub-two".

There is one more notation that must be explained before the first axiom can be stated; it is the notation for "is not a parent of". Normally in mathematics a slash through a symbol denoting a relation is used to denote the negation of the relation; thus " $\neq$ " means "is not equal to". Similarly " $\not{A\!\triangleright}$ " will be used to denote "is not a parent of".

Section 3.2: <u>Axioms Delimiting the Ancestor Relation</u>

The first axiom states merely that no organism is the parent of itself.

<u>Axiom 3.1</u>: For any organism O, $O \mathrel{\not{A\!\triangleright}} O$.

It is desirable to ensure not only that no organism is its own parent but also that no organism is its own ancestor. In order to do this it is necessary first to define the general concept of ancestor. The next definition defines the symbol " $\triangleright$ " to denote the relation "is an ancestor of".

<u>Definition 3.1</u>: $O_1 \rhd O_2$ if and only if $O_1 \mathrel{P\!\!\rhd} O_2$ or there exists a non-empty set of organisms $\{O_3, O_4, O_5, .., O_K\}$ such that $O_1 \mathrel{P\!\!\rhd} O_3 \mathrel{P\!\!\rhd} O_4 \mathrel{P\!\!\rhd} O_5 \ldots \mathrel{P\!\!\rhd} O_K \mathrel{P\!\!\rhd} O_2$.

This definition states that O_1 is an ancestor of O_2 if either O_1 is a parent of O_2 or there is a set of organisms such that O_1 is a parent of O_3, O_3 is a parent of O_4, O_4 is a parent of O_5, and so forth up to O_K is a parent of O_2. Again note that the pointed end of the symbol is pointing at the younger organism.

<u>Axiom 3.2</u>: For any organisms O_1 and O_2, if $O_1 \rhd O_2$, then $O_2 \not\rhd O_1$.

This axiom states that if O_1 is an ancestor of O_2, then O_2 is not an ancestor of O_1. Using these two axioms we can prove that no organism is an ancestor of itself, as is stated in the following theorem.

<u>Theorem 3.1</u>: For any organism O_1, $O_1 \not\rhd O_1$.

We can also prove that if O_1 is an ancestor of O_2, and O_2 is an ancestor of O_3, then O_1 is an ancestor of O_3. This is stated formally in Theorem 3.2.

<u>Theorem 3.2</u>: For any organisms O_1, O_2, and O_3, if $O_1 \rhd O_2$ and $O_2 \rhd O_3$, then $O_1 \rhd O_3$.

The above two axioms give some idea of what is meant by "O_1 is an ancestor of O_2"; the next axiom will give some idea of what is meant by "O_1 is equal to O_2".

Axiom 3.3: For any organisms O_1 and O_2, if $O_1 = O_2$ then 1) if $O_3 \rhd O_1$ then $O_3 \rhd O_2$, and 2) if $O_3 \rhd O_2$ then $O_3 \rhd O_1$.

This axiom states that if $O_1 = O_2$ then every organism in the set of ancestors of O_1 is in the set of ancestors of O_2 and every organism in the set of ancestors of O_2 is in the set of ancestors of O_1. Notice that it does not say that every pair of organisms with this property are equal; if it did then it would imply that if O_1 and O_2 are siblings, then $O_1 = O_2$.

Section 3.3: Definition of Lineage

Now when we discuss natural selection we will be concerned with its action on populations over several generations. Consequently we must eventually decide what we mean by a "population over several generations". Clearly the first step is to define a set containing a specified collection of organisms and its descendants over the generations; we shall call such a set a lineage. The next few definitions will be devoted to explicitly defining this concept.

Definition 3.2: D is a descent if and only if D is an ordered set of organisms $\{O_0, O_1, O_2, \ldots, O_K\}$ such that 1) $K \geq 1$ and 2) for any i such that $0 \leq i < K$, $O_i \lhd O_{i+1}$.

A descent is, thus, a single line of ancestors, where O_0 is a descendant of all of the other organisms in the descent and O_K is an ancestor of all of the other organisms in the descent. In the case of sexually reproducing organisms a single descent will not contain all of the ancestors in the family tree since the descent will contain only one of the parents of each organism. Notice that O_1 is one generation removed from O_0; O_2 is two generations from O_0; and, in general, O_i is i generations removed from O_0. We use this to define "i-descendant".

Definition 3.3: The organism O' is an i-descendant of the set S if and only if there exists an organism O" in S and a descent D such that O' is the first element of D and O" is the i+1st element of D.

Thus a child would be a 1-descendant; a grandchild would be a 2-descendant; a great-grandchild would be a 3-descendant, etc. It will also be convenient to have a term for the opposite relationship; we shall define i-ancestor so that if O' is an i-descendant of O", O" will be an i-ancestor of O'.

Definition 3.4: O" is an i-ancestor of the set S of organisms if and only if there exists O' in S such that O' is an i-descendant of O".

Consider an arbitrary set S of organisms. Denote by R the set containing S and all of its descendants. Then denote the set S by R(0), where the zero indicates that this is to be considered the zeroth generation. Denote the set of all 1-descendants of R(0) by R(1); this will be called the first generation of R. Similarly denote the set of all 2-descendants of R(0) by R(2); this will be called the second generation of R. In general, denote the set of all k-descendants of R(0) by R(k); this will be called the kth generation of R. These concepts will be formalized in the following three definitions.

Definition 3.5: Given any set of organisms R(0) and any positive integer k, the organism O' is in the set R(k) if and only if O' is a k-descendant of R(0).

Definition 3.6: The lineage R associated with a set of organisms R(0) is a set of organisms such that O' is in R if and only if O' is in R(0) or O' is in R(k) for some positive integer k.

Definition 3.7: The kth generation of the lineage R is a set of organisms such that O' is in the kth generation of the lineage R if and only if O' is in R(k).

Thus we now have a word, lineage, which denotes a set of organisms plus all of its descendants.

Section 3.4: Definition of Subset and Other Set Theoretic Notations

The primary notion of set theory, that of set, has already been used extensively without any explanation of what is meant by it. This was possible because the meaning of "set" within set theory is very close to its meaning in its everyday usage. However, in order to go further in this discussion of lineages we will need to use a few notions from set theory that are not self-explanatory; therefore this section will be used to describe or define them.

We have above defined R(k) as the set of all k-descendants of R(0). But suppose R(0) has no k-descendants; is it still legitimate to call R(k) a set? Yes, it is; such a set containing no elements is called the null set. The null set will be denoted here by the symbol "$\emptyset$"; thus if R(0) has no k-descendants $R(k) = \emptyset$, or, to put it in words, R(k) is equal to the null set.

Now we should make explicit what will be meant by saying of two sets, S_1 and S_2, that $S_1 = S_2$.

Definition: $S_1 = S_2$ if and only if there exists a one-to-one correspondence between organisms O' in S_1 and O" in S_2 such that corresponding organisms are equal.

We will often have occasion to use the concept of a part of a set. For example, we may wish to say that one part of a set is superior to another part of the set. A part of a set is called, in set theory, a subset of the set. This is defined as follows.

<u>Definition</u>: S_1 is a subset of S if and only if every organism O in S_1 is also in S.

<u>Notation</u>: $S_1 \subset S$ means S_1 is a subset of S.

Now suppose that $R_1(k)$ is the set of all organisms in R(k) which have claws; then $R_1(k)$ is a subset of R(k). If no organisms in R(k) have claws, then $R_1(k)$ contains no organisms and so $R_1(k) = \emptyset$. If all of the organisms in R(k) have claws, then $R_1(k) = R(k)$; notice that a subset need not be smaller than the set. At times it will be necessary to stipulate that a particular subset S_1 is a subset of S but that it is not equal to S; that is, that there is at least one organism which is in S and not in S_1. To stipulate this we will use the following notation.

<u>Notation</u>: $S_1 \subsetneqq S$ means that S_1 is a subset of S and S_1 is not equal to S.

For example, if $R_1(k)$ is, as before, the set of all organisms in R(k) which have claws, then the stipulation $R_1(k) \subsetneqq R(k)$ would guarantee that there is at least one organism in R(k) which does not have claws.

Now suppose $R_2(k)$ is the set of all organisms in R(k) which have teeth. Then the set of all organisms in R(k) which have either teeth or claws (or both) is the set of all organisms which are in either $R_1(k)$ or $R_2(k)$. It will be useful to have a notation for a set which is the sum (or, as it is usually called, the union) of two given sets. Below we define the union of two sets and then give the notation which is used for it.

Definition: S_3 is the union of S_1 and S_2 if and only if every organism that is in S_3 is in either S_1 or S_2 and every organism that is in either S_1 or S_2 is in S_3.

Notation: $S_1 \cup S_2$ denotes the set S_3 which is the union of S_1 and S_2.

Suppose an organism O' has both teeth and claws. Then O' is in both $R_1(k)$ and $R_2(k)$. The set of all organisms which are in both of two sets is called the intersection of those two sets. This set is defined below.

Definition: S_3 is the intersection of S_1 and S_2 if and only if every organism that is in S_3 is in both S_1 and S_2 and every organism that is in both S_1 and S_2 is in S_3.

Notation: $S_1 \cap S_2$ denotes the set S_3 which is the intersection of S_1 and S_2.

It will often be necessary to discuss the set of all organisms which are in a set S but are not in a certain subset S_1. For example, the set of all organisms in R(k) which do not have claws is the set of all organisms which are in R(k) but are not in $R_1(k)$. This set is called the complement of $R_1(k)$ with respect to R(k); this concept is defined as follows.

Definition: S_3 is the complement of S_1 with respect to S if and only if every organism that is in S_3 is in S and is not in S_1, and every organism that is in S and is not in S_1 is in S_3.

Notation: $S - S_1$ denotes the set S_3 which is the complement of S_1 with respect to S.

Thus the set of all organisms in $R(k)$ which do not have claws may be denoted by $R(k) - R_1(k)$.

Section 3.5: Descendants of a Subset

Now it is possible to define a notation for the set of all i-descendants of a subset of $R(j)$ which will make clear its connection with the j^{th} generation. This will be useful when it is necessary to compare, e.g. the descendants of those organisms which have claws with the descendants of those organisms which do not have claws.

Notation: Let $R_1(j)$ be a subset of $R(j)$. Let R_{1j} be the lineage associated with the set of organisms $R_1(j) = R_{1j}(0)$. Then $R_{1j}(i)$ is the i^{th} generation of the lineage R_{1j}, and $R_{1j}(i)$ is a subset of the $j + i^{th}$ generation of the lineage R. Define the set $R_1^j(j+i)$ by the equation $R_1^j(j + i) = R_{1j}(i)$, where i is a non-negative integer.

This notation, $R_1^j(k)$, permits a brief designation of the set of all organisms in the k^{th} generation of R which are descendants of $R_1(j)$. For example, suppose we wished to say that the set of descendants of a particular subset $R_1(j)$ of $R(j)$ are superior in every generation after j to the set of organisms in their generation; then we simply say that for all $k > j$, $R_1^j(k)$ is superior to $R(k) - R_1^j(k)$.

Now we will use the concepts developed so far to prove two theorems that will be of use in later chapters.

Suppose that the population $R(j)$ contains a subset $R_1(j)$ of organisms containing a certain "good" gene. This gene will be selected for and will spread throughout the population; that is, after a certain number, k', of generations every organism of the population $R(j+k')$ will have the gene. If mutation to this gene is sufficiently rare, we may expect that every organism in $R(j+k')$ is a descendant of the original subset $R_1(j)$; that is, every organism in $R(j+k')$ is also in $R_1^j(j+k')$. Now we would like to be able to say that in this case every organism in later generations must also be a descendant of $R_1(j)$; that is, if $R(j+k') = R_1^j(j+k')$, then for all $k \geq j+k'$, $R(k) = R_1^j(k)$. This is clearly a general property of sets of descendants and can be stated as a general theorem about descendants, without reference to "good" genes and selective forces. We will then have the following general statement: if there exists a generation m such that all organisms in $R(m)$ are descendants of $R_1(j)$, then for all $k \geq m$ all organisms in $R(k)$ will be descendants of $R_1(j)$. This is stated formally in Theorem 3.4.

It is easier to prove Theorem 3.4 if another theorem is proved first. This theorem states that if there are two subsets of $R(m)$, $R_1^{j1}(m)$ and $R_2^{j2}(m)$, such that $R_1^{ji}(m)$ is a subset of $R_2^{j2}(m)$, then for all generations $k \geq m$ the set of descendants of $R_1^{j1}(m)$ will be a subset of the set of descendants of $R_2^{j2}(m)$. (In this statement j1 and j2 are used instead of simply j in order to allow for the possibility that the generation in which R_1 was originally defined was not the same as the generation for which R_2 was originally defined.) For example, if the descendants of Jones and Brown intermarry so that by the m^{th} generation all descendants of Jones are also descendants of Brown, then there cannot be, in subsequent generations, any descendants of Jones which are not descendants of Brown. This is stated formally in the following theorem.

<u>Theorem 3.3</u>: If $0 \leq j1 \leq m$, $0 \leq j2 \leq m$, and $R_1^{j1}(m) \subset R_2^{j2}(m)$, then for all $k \geq m$, $R_1^{j1}(k) \subset R_2^{j2}(k)$.

<u>Theorem 3.4</u>: If $0 \leq j \leq m$ and $R_1^{j}(m) = R(m)$, then for all $k \geq m$ $R_1^{j}(k) = R(k)$.

Section 3.6: Axiom Delimiting Lineage

The next axiom is not a statement about the ancestor relation, as the previous ones have been, but a statement about the world in which the organisms live. It states simply that for any lineage R and any generation k, the number of organisms in $R(k)$ is finite.

It will frequently be necessary in succeeding chapters to refer to the number of organisms in a particular generation of a particular lineage. We shall, therefore, define a notation for this concept so that it may be referred to more easily.

Notation: $N(R,k)$ is the number of organisms in $R(k)$.

Axiom 3.4: For any lineage R there exists a positive integer M_R such that, for any generation k, $N(R,k) \leq M_R$.

M_R, therefore, is an absolute upper bound to the number of organisms in any one generation of R. It should not be confused with the temporary upper bounds imposed by, e.g., climatic conditions over a long succession of generations but which may change if the climate changes. For a given lineage M_R is fixed for all time, and no amount of environmental change and no number of "good" mutations will allow it to be exceeded. The existence of M_R may be considered as being due to the fact that there is a limited amount of matter in the world, and therefore there is a limitation to the number of organisms that can be made out of that matter.

Section 3.7: Definition of Biological Universe

It would be possible to investigate further the structure specified for these sets of organisms by these axioms and to prove more theorems concerning it. However the primary purpose of this chapter was to set forth the axioms defining what we will call a Biological Universe and this purpose has been accomplished. We shall, therefore, close this chapter with a definition of Biological Universe.

Definition: A Biological Universe is a set B of organisms and two relations, $A\!\!\triangleright$ and $=$, such that axioms 3.1 through 3.4 are true statements about them.

Notation: $(B, A\!\!\triangleright, =)$ denotes a Biological Universe.

CHAPTER 3 : APPENDIX

A Biological Universe $(B, A\triangleright, =)$ is a set B of organisms and two relations, $A\triangleright$ and $=$, such that the following four axioms hold:

Axiom 3.1: For any O in B, $\sim(O\ A\triangleright\ O)$.

($\sim$ is here used as the symbol for the logical negation.)

Definition 3.1: $O_1 \triangleright O_2$ if and only if $O_1\ A\triangleright\ O_2$ or there exists a non-empty set of organisms $\{O_3, O_4, O_5, \ldots, O_k\}$ such that $O_1\ A\triangleright\ O_3\ A\triangleright\ O_4\ A\triangleright\ O_5\ A\triangleright \ldots A\triangleright O_k\ A\triangleright\ O_2$.

Axiom 3.2: For any O_1 and O_2 in B, if $O_1 \triangleright O_2$, then $\sim(O_2 \triangleright O_1)$.

Axiom 3.3: For any O_1 and O_2 in B, if $O_1 = O_2$ then: 1) if there exists O_3 in B such that $O_3 \triangleright O_1$, then $O_3 \triangleright O_2$; and 2) if there exists O_4 in B such that $O_4 \triangleright O_2$, then $O_4 \triangleright O_1$.

Definition 3.2: D is a descent if and only if D is an ordered set of organisms in B $\{O_0, O_1, O_2, \ldots, O_k\}$ such that; 1) $k \geq 1$; and 2) for any integer i such that $0 \leq i < k$, $O_i\ A\triangleright\ O_{i+1}$.

Definition 3.3: The organism O' is an i-descendant of the set S if and only if there exists an organism O" in S and a descent D such that O' is the first organism of D and O" is the $i+1^{st}$ organism of D.

Definition 3.4: O" is an i-ancestor of the set S of organisms if and only if there exists O' in S such that O' is an i-descendant of O".

Definition 3.5: Given any set of organisms $R(O)$ and any positive integer k, the organism O' is in the set $R(k)$ if and only if O' is a k-descendant of $R(O)$.

Definition 3.6: The lineage R associated with a set of organisms $R(O)$ is a set of organisms such that O' is in R if and only if O' is in $R(O)$ or O' is in $R(k)$ for some positive integer k.

Definition 3.7: The k^{th} generation of the lineage R is a set of organisms such that O' is in the k^{th} generation of the lineage R if and only if O' is in $R(k)$.

Notation: $N(R,k)$ is the cardinal number of the set $R(k)$.

Axiom 3.4: For any lineage R there exists a positive integer M_R such that, for any generation k, $N(R,k) \leq M_R$.

Some theorems which can be proved using these axioms follow:

Theorem 3.1: For any organism O_1, $O_1 \not\triangleright O_1$.

Proof: Suppose $O_1 \triangleright O_1$. Then, by definition, either (1) $O_1 \mathrel{A\!\triangleright} O_1$ or (2) there exists a non-empty set $\{O_2, O_3, \ldots, O_k\}$ such that $O_1 \mathrel{A\!\triangleright} O_2 \mathrel{A\!\triangleright} O_3 \ \ldots \mathrel{A\!\triangleright} O_k \mathrel{A\!\triangleright} O_1$. By Axiom 3.1, $O_1 \mathrel{\cancel{A\!\triangleright}} O_1$, so (1) cannot hold. But if (2) holds, then $O_1 \triangleright O_2$ and $O_2 \triangleright O_1$, which cannot happen by Axiom 3.2. Therefore, since assuming that $O_1 \triangleright O_1$ leads to a contradiction, $O_1 \not\triangleright O_1$.

Theorem 3.2: For any organisms O_1, O_2, and O_3 in B, if $O_1 \triangleright O_2$ and $O_2 \triangleright O_3$, then $O_1 \triangleright O_3$.

Proof: $O_1 \triangleright O_2$ implies, by definition, that either (1) $O_1 \mathrel{A\!\!\triangleright} O_2$ or (2) there exists a descent $\{O_4, O_5, O_6, \ldots, O_k\}$ such that $O_1 \mathrel{A\!\!\triangleright} O_4 \mathrel{A\!\!\triangleright} O_5 \mathrel{A\!\!\triangleright} O_6 \ldots \mathrel{A\!\!\triangleright} O_k \mathrel{A\!\!\triangleright} O_2$. Similarly, $O_2 \triangleright O_3$ implies that either (1) $O_2 \mathrel{A\!\!\triangleright} O_3$ or (2) there exists a descent $\{O_4', O_5', \ldots, O_k'\}$ such that $O_2 \mathrel{A\!\!\triangleright} O_4' \mathrel{A\!\!\triangleright} O_5' \ldots \mathrel{A\!\!\triangleright} O_k' \mathrel{A\!\!\triangleright} O_3$. If (1) holds for both $O_1 \triangleright O_2$ and $O_2 \triangleright O_3$, then $O_1 \mathrel{A\!\!\triangleright} O_2 \mathrel{A\!\!\triangleright} O_3$, and the set $\{O_2\}$ is a descent such that (2) holds for O_1 and O_3; therefore in this case $O_1 \triangleright O_3$. If (1) holds for $O_1 \triangleright O_2$ and (2) holds for $O_2 \triangleright O_3$, then $\{O_2, O_4', O_5', \ldots, O_k'\}$ is a set such that (2) holds for O_1 and O_3; therefore in this case $O_1 \triangleright O_3$. If (2) holds for both $O_1 \triangleright O_2$ and $O_2 \triangleright O_3$, then $\{O_4, O_5, \ldots, O_k, O_2, O_4', O_5', \ldots, O_k'\}$ is a set such that (2) holds for O_1 and O_3; therefore in this case $O_1 \triangleright O_3$. We have shown that in all possible cases $O_1 \triangleright O_3$.

Notation: Let $R_1(j)$ be a subset of $R(j)$. Let R_{1j} be the lineage associated with the set of organisms $R_1(j) = R_{1j}(0)$. Then $R_{1j}(i)$ is the i^{th} generation of the lineage R_{1j} and is a subset of the $j + i^{th}$ generation of the lineage R. Define the set $R_1^j(k)$ by the equation $R_1^j(j+i) = R_{1j}(i)$, where i is a non-negative integer.

Theorem 3.3: If $0 \leq j1 \leq m$, $0 \leq j2 \leq m$, and $R_1^{j1}(m) \subset R_2^{j2}(m)$, then for all $k \geq m$, $R_1^{j1}(k) \subset R_2^{j2}(k)$.

Proof: Suppose O' is in $R_1^{j1}(k)$ for some $k > m$. We must show that it is also in $R_2^{j2}(k)$. O' in $R_1^{j1}(k)$ implies that there exists a descent D of length $k - j1 + 1$ such that the first organism in D is O' and the last organism in D is in $R_1^{j1}(j1)$. The last $j1 - m + 1$ organisms of this descent provide a descent D' such that the first organism, O'_{j1} is in $R_1^{j1}(m)$. Therefore, since $R_1^{j1}(m) \subset R_2^{j2}(m)$, O' is in $R_2^{j2}(m)$. By definition of $R_2^{j2}(m)$ there exists a descent D" such that the first organism in D" is O'_{j1} and the last organism in D" is in $R_2^{j2}(j2)$. If we let the descent D be the descent whose first $k - m + 1$ organisms are the first $k - m + 1$ organisms of D and whose last $m - j2 + 1$ organisms are the organisms of D", then D is a descent whose first organism is O' and whose last organism is in $R_2^{j2}(j2)$, thus proving that O' is a descendant of $R_2^{j2}(j2)$. Therefore O' is in $R_2^{j2}(k)$.

We have taken an arbitrary organism O' in $R_1^{j1}(k)$ and shown that it is in $R_2^{j2}(k)$. Therefore $R_1^{j1}(k) \subset R_2^{j2}(k)$.

Theorem 3.4: If $0 \leq j \leq m$ and $R_1^j(m) = R(m)$, then for all $k \geq m$, $R_1^j(k) = R(k)$.

Proof: We first note that R(m) can be considered to be a sublineage of itself; that is, $R(m) = R_0^0(m)$. Since, by the definition of subset, $R_1^j(m) = R(m)$ implies that

$R_1^j(m) \subset R(m)$, theorem 3.3 can be used to give $R_1^j(k) \subset R(k)$. Similarly, $R_1^j(m) = R(m)$ implies that $R(m) \subset R_1^j(m)$, and by theorem 3.3 this implies that $R(k) \subset R_1^j(k)$. But, for any sets S' and S'', $S' \subset S''$ and $S'' \subset S'$ implies that $S' = S''$. Therefore $R_1^j(k) = R(k)$.

CHAPTER 4: DARWINIAN UNIVERSES

In the first chapter of this thesis Darwin's summary of the theory of natural selection was quoted and it was stated that his theory is still considered to be essentially correct. In this chapter we shall convert the important constituents of his statement of the theory into explicitly stated axioms and derive some of their consequences.

Section 4.1: Populations

Clearly when Darwin spoke of "organic beings" and their "offspring" he was assuming the existence of a set of organisms and an ancestor relation with the properties discussed in the previous chapter. In particular, when he says(16) "if there be owing to their geometric rate of increase, a severe struggle for life," he is assuming the property given by Axiom 3.4; for without an upper limit on the number of organisms in a generation, there is no reason for a geometric rate of increase leading to a severe struggle for life. Therefore it will be necessary to state an axiom specifying that the objects of natural selection are in a Biological Universe.

Single organisms are not the objects of natural selection; selection is a process which changes the composition of populations and it must be discussed in terms of populations. Population is one of the elementary concepts of natural selection, so it will be an undefined term in this axiom system. Like all undefined terms its meaning will be delimited only by the statements made in the axioms concerning its properties.

Intuitively speaking, a population is a lineage in which the different sublineages are tied together by the law of the survival of the fittest and in which there is sufficient hereditary variation. It should be recognized that a lineage is not necessarily composed of members of only one species; the associated set R(O) may have contained members of several species and in this case the lineage R will consist of several non-interbreeding sublineages. On the other hand, the fact that the law of the survival of the fittest holds guarantees that there is some relation between the different sublineages in a population (possibly competition for resources). This law does not necessarily hold for every lineage, for if a less fit part of the lineage accidentally found new and unexploited territory and thereafter had no contact with the rest of the lineage, it might survive and flourish although continuing to be less fit; thus it is clear that not all lineages are populations. It should also be clear that not all sets of organisms which are populations in the sense in which the word is used here are populations in the sense in which the word is used in population genetics. But all sets of organisms which are populations in the sense in which the word is used in population genetics should be populations in the sense in which the word is used here. The word is used here to denote a larger variety of sets of organisms than it denotes in population genetics.

Axiom 4.1: For any population R, R is a lineage in $(B, A\triangleright, =)$.

Section 4.2: Fitness of an Organism

Clearly we cannot talk about natural selection without using the concept of fitness, but this concept, while very intuitive, is remarkably hard to define explicitly. Those who must define it explicitly (e.g. Fisher,(17); Feller,(18) and Hamilton,(19)) generally use the expected number of offspring; that is, O' is fitter than O" if the expected number of offspring of O' is greater than the expected number of offspring of O". But this is not the intuitive concept of fitness; it is merely a consequence of the intuitive fitness. Furthermore, it is a consequence of intuitive fitness only when the population is subject to selection. (If the organism is in a population which is being artificially selected by an experimenter for, e.g. low bristle number, it may have a very low expected number of offspring even though its intuitive fitness is much higher than that of the other organisms in the population.

It may be argued that this organism does indeed have a low fitness in the environment created by the experiment, but this only makes it more obvious that fitness is not independent of selection.) Thus the definition should be: the fitness of an organism is equal to the number of offspring of the organism expected when the population is under the operation of natural selection. If we then state natural selection in terms of "survival of the fittest" we will find ourselves in the well-known dilemma described as follows by Mayr.(20)

> "Darwin...has therefore been accused of tautological (circular) reasoning: 'What will survive? The fittest. What are the fittest? Those that survive.' To say that this is the essence of natural selection is nonsense! To be sure, those individuals that have the most offspring are by definition (Lerner, 1959) the fittest ones. However, this fitness is determined (statistically) by their genetic constitution..... A superior genotype has a greater probability of leaving offspring than has an inferior one. Nstural selection, simply, is the differential perpetuation of genotypes."

Mayr has ended in the same circle in which he started; we have only to ask: "which are the superior genotypes?" But he is right to be in this circle; his error lies in the (unexpressed) assumption that arguments which are tautological are worthless; since he knows that the concept of natural selection is not worthless, he concludes that it is nonsense to call it tautological. But, in fact, properly controlled tautological arguments can have great power and real explanatory value. Any axiomatized theory can be considered to be in the form "if axioms, then theorems;" this implication is true regardless of the truth of either the axioms or the theorems; therefore, it is, by definition, tautological. Euclidean geometry is an example of such a tautological theory, yet it is clearly not worthless.

If we consider the concept of "point" in Euclidean geometry and subject a mathematician to the catechism used above for the concept of fitness, we will hear: "What satisfies the Euclidean axioms? Points. What is a point? Something which satisfies the Euclidean axioms." Notice that the mathematicians' reasoning is just as circular as the biologists'. But, it may be protested, everyone knows what a point is! Indeed it is just as true to say that everyone knows what fitness is; and it is just as difficult to explicitly define "point" as to explicitly define "fitness".

This difficulty has been met in geometry by the device of explicitly stating that point is an undefined concept. There is an intuitive concept of what a point is, and this intuitive concept is used to decide what statements about points are likely to be true. But when these statements are being formally proved, the only information that can be used about points is the fact that they are entities which satisfy the Euclidean axioms.

The difficulty in defining fitness will be met in exactly the same way. It will be an undefined concept, denoted by f(O), about which we can say only that it satisfies the axioms of the Darwinian Universe. But for purposes of heuristic thinking we can consider that f(O) exactly corresponds to the intuitive concept of a measure of the fitness of the organism in the environment in which it spends its life.

It is intuitively reasonable that any organism has a positive fitness; it may be very small but the fact that the organism exists long enough to be the object of discussion implies that its fitness is not zero. Therefore we assert the following property of f(O) as an axiom.

Axiom 4.2: For any organism O, f(O) is a positive real number.

Section 4.3: Fitness with Respect to a Set of Organisms

Normally the intrinsic fitness of an organism is not by itself important for natural selection; what is important is the fitness of the organism relative to the fitness of the other organisms in some population. Therefore we shall define the fitness of O relative to R(k) as the ratio of its fitness to the sum of the fitnesses of all of the organisms in R(k).

Definition 4.1:

$$F(O,R,k) = \frac{f(O)}{\sum\limits_{O_i \text{ in } R(k)} f(O_i)} \qquad \text{if } O \text{ is in } R(k)$$

$$= 0 \qquad \text{if } O \text{ is not in } R(k)$$

We have, thus, defined a new function $F(O,R,k)$ in terms of the fitness function $F(O)$. Note that with this definition, if O' and O'' are both in $R(k)$, $F(O',R,k) > F(O'',R,k)$ if and only if $f(O') > f(O'')$; thus the definition has not changed the relative fitnesses of any two organisms.

Theorems 4.1 and 4.2 follow immediately from this definition and Axiom 4.2.

Theorem 4.1: For any O' in $R(k)$, $0 < F(O',R,k) \leq 1$.

Theorem 4.2: $F(O',R,k) = 0$ if and only if O' is not in $R(k)$.

Theorem 4.1 asserts that if O is in $R(k)$ then the fitness of O relative to the fitness of all organisms in $R(k)$ is always between 0 and 1. On the other hand, if O is not in $R(k)$ its fitness relative to $R(k)$ is always 0; therefore if O' is in $R(k)$ and O'' is not in $R(k)$, $F(O'',R,k)$, which is equal to 0, is always less than $F(O',R,k)$ even though $f(O'')$ may be greater than $f(O')$. However, if we wish to compare two such organisms using F, we can do so by defining $R'(0) = R(k) + O''$; then $F(O',R',0) > F(O'',R',0)$ if and only if $f(O') > f(O'')$.

It will be useful to be able to discuss the fitness of parts of a population relative to the whole population, so we shall define the fitness of a part of a generation relative to the whole generation. Consider two populations R and R'. We shall usually be interested in the case when R' is a subpopulation of R, but it will be useful to have fitness defined for the most general case. To do this it will be necessary to use $R'(k) \cap R(k)$, the set of organisms which are in both $R'(k)$ and $R(k)$.

Definition 4.2: Let $R^*(k) = R'(k) \cap R(k)$. Then

$$F(R',R,k) = \left\{ \sum_{O \text{ in } R'(k)} F(O,R,k) \right\} \frac{N(R,k)}{N(R^*,k)} \quad \text{if } R^*(k) \neq \emptyset$$

$$= 0 \quad \text{if } R^*(k) = \emptyset$$

The purpose of multiplying by $N(R,k)/N(R^*,k)$ is to make $F(R',R,k)$ an average fitness; otherwise the larger the subpopulation the greater the fitness. $F(R',R,k)$ is such that, if the subpopulation R' is superior in fitness in the generation k to the population R, then $F(R',R,k) > 1$. On the other hand, if R' is inferior in this generation, then $F(R',R,k) < 1$. Some other interesting properties of F will now be stated as theorems.

Theorem 4.3: $F(R',R,k) = 0$ if and only if $R'(k) \cap R(k) = \emptyset$.

Theorem 4.4: If $R(k) \neq \emptyset$, then $F(R,R,k) = 1$.

Notation: In $F(R-R',R,k)$, $R-R'$ denotes the set $R(k) - R'(k)$.

Theorem 4.5: Let R and R' be such that $\emptyset \neq R'(k) \cap R(k) \neq R(k)$. Then $F(R',R,k) > 1$ if and only if $F(R-R',R,k) < 1$.

Theorem 4.6: Let R and R' be such that $\emptyset \neq R'(k) \cap R(k) \neq R(k)$. Then $F(R',R,k) = 1$ if and only if $F(R-R',R,k) = 1$.

Theorem 4.7: Let R and R' be such that $\emptyset \neq R'(k) \cap R(k) \neq R(k)$. Then $F(R',R,k) > F(R,R,k)$ if and only if $F(R',R,k) > F(R-R',R,k)$.

Theorem 4.3 states that if $F(R',R,k) = 0$ then there are no organisms that are in both $R'(k)$ and $R(k)$; it states further that if there are no organisms that are in both $R'(k)$ and $R(k)$, then $F(R',R,k) = 0$. Theorem 4.4 states that any population is exactly as fit as itself. Theorem 4.5 asserts that if the fitness of a subpopulation is greater than the fitness of the population as a whole in generation k (i.e. if $R'(k)$ has more than its fair share of the more fit organisms), then the fitness of the remainder of the population must be less than the fitness of the population as a whole (i.e. the remainder of the population must contain in that generation less than its fair share of the more fit organisms). Theorem 4.6 asserts that if $R'(k)$ contains exactly its fair share of the more fit organisms, then the remainder of the generation must also contain exactly its fair share. Theorem 4.7 asserts that if $R'(k)$ has more than its fair share of the fitter organisms then its average fitness is greater than the average fitness of the population as a whole. All of these assertions are straightforward, intuitive -- even trivial, and they are meant to be; these theorems prove that F has the qualities that a fitness function should have.

Section 4.4: Survival of the Fittest

Now that the concepts of fitness that shall be used have been specified, it is possible to convert the most important constituent of Darwin's theory into an axiom.(21)

> "assuredly individuals thus characterized by useful variations will have the best chance of being preserved in the struggle for life".

This is not, of course, a statement which follows with logical necessity from the other elements of his argument; it is a statement about the type of universe in which the events are assumed to take place. It is easy to imagine a universe in which this statement is not true (e.g. a universe in which the individuals death or reproduction is determined by an omnipotent god from a table of random numbers) and it would not even be difficult to approximate such a universe in the laboratory. Since the statement is not necessarily true in all possible universes, it is necessary to explicitly assume that it is true in a Darwinian Universe. That is, it must be stated as an axiom.

But first it is necessary to define a concept which must be used in the statement of the axiom. It will be a rather complicated definition, for the concept is not simple, but it is important to understand it as it contains the secret of the hidden compartment from which all subsequent rabbits will be produced.

It is clear that, in the world which we would like our axioms to describe (i.e. the world in which we live), the better organism does not always win; the most that can be said is that it wins most of the time. The usual way to handle this uncomfortable fact mathematically is to use the theory of probability, that is, to state that the better organism has a higher probability of winning. We shall, instead, state that in the long run the fitter set of organisms will win, if it stays fitter long enough. It may not increase at the expense of the less fit in every generation, but it will do so over any sufficiently long succession of generations. In order to work with this it is necessary to be able to break up any long succession of generations into a set of 'sufficiently long' successions of generations. For example, if it is necessary to consider the generations between 100 and 1000, we shall define a partition, p(100,1000) of these generations as a set of smaller successions of generations which are composed of successive generations and which completely cover, without overlapping except at the ends, the generations between 100 and 1000; that is, each generation between 100 and 1000 is in one and only one of the smaller successions. An example of a partition of

100,1000 is $\{(100, 120), (120, 196), (196, 254), (254, 255), (255, 847), (847, 1000)\}$. The following definition of partition makes this more explicit.

Definition 4.3: For any integers j_1 and j_2, a partition, $p(j_1,j_2)$, of j_1,j_2 is a set of pairs of integers such that:

(1) for any pair (k_1,k_2) in $p(j_1,j_2)$ either $k_1 = j_1$ or there exists exactly one pair (k_1',k_2') in $p(j_1,j_2)$ such that $k_2' = k_1$;

(2) for any pair (k_1,k_2) in $p(j_1,j_2)$ either $k_2 = j_2$ or there exists exactly one pair (k_1'',k_2'') in $p(j_1,j_2)$ such that $k_1'' = k_2$;

(3) there exists exactly one pair (k_1,k_2) in $p(j_1,j_2)$ such that $k_1 = j_1$;

(4) there exists exactly one pair (k_1,k_2) in $p(j_1,j_2)$ such that $k_2 = j_2$;

(5) for any pair (k_1,k_2) in $p(j_1,j_2)$ there exists no pair (k_1',k_2') in $p(j_1,j_2)$ such that $k_1' < k_1 < k_2'$ or $k_1' < k_2 < k_2'$;

(6) for any pair (k_1,k_2) in $p(j_1,j_2)$, $j_1 \leq k_1 < k_2 \leq j_2$.

Notice that there are a great many different partitions of any j_1,j_2. It is important that every generation between j_1 and j_2 is included in any partition; this fact is not stated in the definition, but it may be proved as a theorem.

Theorem 4.8: For any integer i such that $j_1 \leq i \leq j_2$ and for any partition $p(j_1,j_2)$, there exists a pair (k_1,k_2) in $p(j_1,j_2)$ such that $k_1 \leq i \leq k_2$.

Notation: Let $N(p(j_1,j_2))$ denote the number of pairs in the partition.

Now, at last, it is possible to state the survival of the fittest axiom.

Axiom 4.3: (Survival of the Fittest): For any population R, if $R_1^m(j_1)$ is a subset of $R(j_1)$ and there exists an $\Omega > 0$ such that $F(R_1^m,R,k) > F(R-R_1^m,R,k) + \Omega > \Omega$ for all k between j_1 and j_2, then if $\Omega(j_2-j_1) \geq 1$ there exists a partition $p(j_1,j_2)$ such that for every pair (k_1,k_2) in the partition

$$N(R_1^m,k_2) - N(R-R_1^m,k_2) > N(R_1^m,k_1) - N(R-R_1^m,k_1)$$

and $N(p(j_1,j_2)) \geq \Omega(j_2-j_1)$.

Suppose that in generation k_1 there were exactly two more organisms in $R_1^m(k_1)$ than in $R(k_1) - R_1^m(k_1)$; that is $N(R_1^m,k_1) - N(R-R_1^m,k_1) = 2$; then according to the axiom, $N(R_1^m,k_2) - N(R-R_1^m,k_2) > 2$, which implies that during the generations between k_1 and k_2 the number of organisms in R_1^m has increased relative to the number of organisms in the remainder of the population. Or, in general, the axiom states that for every pair (k_1,k_2) in the partition, the number of organisms in R_1^m has increased during the generations between k_1 and k_2 relative to the number of organisms in the remainder of the population. It does not state that the number of organisms in R_1^m has increased, for the inequality would still be true if both

R_1^m and $R-R_1^m$ were decreasing in number as long as $R-R_1^m$ was decreasing faster than R'. The axiom further states that the number of such pairs (k_1,k_2) is at least equal to $\Omega(j_2-j_1)$.

Now let us consider the first part of the axiom. Remember that, according to theorem 4.7, $F(R',R,k) > F(R-R',R,k)$ implies that the average fitness of $R'(k)$ is greater than the average fitness of the population as a whole. Thus this axiom says that a subpopulation whose average fitness is greater than the average fitness of the population as a whole for a sufficiently long period of time will increase in numbers relative to the population as a whole.

Notice that there is no assumption that R_1^m will increase in absolute numbers; natural selection will occur even when the population as a whole is decreasing. It is necessary to state the axiom so that this will be true, since in nature the most effective selection often takes place while the population as a whole is decreasing and in spite of the fact that the favoured population is also decreasing.

Notice also that the axiom does not state that the favoured population gains (relatively) in every generation; it is necessary to avoid stating this since, in the universe which the axioms should describe, there is an element of chance which occasionally allows a less fit subpopulation to gain on the remainder of the population. What the axiom does state is that if the fitness difference (Ω) multiplied by the number of generations in which it exists (j_2-j_1) is large enough, then selection will occur.

A close look at the axiom shows that it will guarantee an average gain of Ω organisms per generation, though it does not rule out the possibility that the gain is much greater. The reason for this very low average gain is that the axiom does not state that the average gain per generation is a function of the size of the populations as well as of the fitness difference and the length of time. It would be possible to state this in the axiom, but at present this would complicate matters unnecessarily; natural selection would be seen to proceed faster if this were stated, but speed is not important; what is important is the question of what happens when natural selection proceeds.

Section 4.5: Some Theorems on the Fate of Superior and Inferior Subpopulations

Theorem 4.9: If $R_1(m)$ is a subset of $R(m)$ and there exists a $\Omega > 0$ such that $F(R_1^m, R, k) > F(R-R_1^m, R, k) + \Omega$ for all k such that $k \geq m$ and $R_1^m(k) \neq R(k)$, then there exists an integer t such that $R(t) = R_1^m(t)$.

This theorem states that if the descendants of $R_1(m)$ are better than the remainder of the population for long enough, then there will be a generation t such that all organisms in the population R after the generation t are descendants of $R_1(m)$; i.e. the descendants of $R_1(m)$ will have completely taken over the population by the generation t. Note that it does not state that R_1^m has eliminated another subpopulation; in sexually reproducing populations there is always the possibility that the inferior population has ensured some descendants by interbreeding with the superior population. (The axiom was carefully worded to avoid stating that any subpopulation would decrease; survival of the fittest is not the same as elimination of the unfittest.) However in asexual populations, or in populations with two non-interbreeding subpopulations of which one is superior to the other, it can be asserted that the inferior population will be eliminated. This will be stated in theorem 4.10.

Notation: If R_1^m is a subpopulation of R which fulfills the conditions of theorem 4.9 and t is the generation guaranteed by the theorem, then we shall call t the takeover generation of R_1^m with respect to R and we shall denote it by $t(R_1^m, R)$.

Definition 4.4: R_1^{j1} and R_2^{j2} are non-interbreeding for $i = k$ if and only if $R_1^{j1}(i) \cap R_2^{j2}(i) = \emptyset$.

This simply states that two populations are non-interbreeding if they have no descendants in common.

Theorem 4.10: If $R(k) = R_1^m(k) \cup R_2^m(k)$, $R_1^m(k)$ and $R_2^m(k)$ are non-interbreeding for $k > m$, and there exists $\Omega > 0$ such that $F(R_1^m, R, k) > F(R_2^m, R, k) + \Omega$ for all k such that $k \geq m$ and $R_1^m(k) \neq R(k)$, then $R_2^m(t(R_1^m, R)) = \emptyset$.

This theorem states that by the time of the takeover generation R_2^m will have been eliminated. Notice that we are beginning to see differences between the way natural selection works on sexually reproducing populations and the way it works on asexually reproducing populations. In asexual populations it completely eliminates inferior populations; in sexual populations it simply ensures that after a certain time all of the population will be descendants of the superior subpopulation. This is, in fact, an indication of the greater flexibility of sexual populations in storing variability.

Theorem 4.11: If there exists an $\Omega > 0$ and a number b and R_1^m such that $F(R_1^m, R, k) > F(R - R_1^m, R, k) + \Omega$ for all k such that $N(R_1^m, k)/N(R, k) \leq b$ then there exists an integer j such that $N(R_1^m, j)/N(R, j) \geq b$.

This theorem describes what happens when the advantage of the subpopulation R_1^m is density dependant. It asserts that if R_1^m is a subpopulation which is superior to the remainder of the population as long as it constitutes less than the proportion b of the population, then R will attain that proportion. If we further assert that R does not interbreed with the rest of the population and that it is inferior to the rest of the population when it constitutes more than the proportion b, we can assert that the proportion of R_1^m to R will either stabilize at b or oscillate around b. This is stated in the next theorem.

Theorem 4.12: If $R(k) = R_1^m(k) \cup R_2^m(k)$ for all $k \geq m$, R_1^m and R_2^m are non-interbreeding for all $k \geq m$, and there exist numbers b and $\Omega > 0$ such that (1) $F(R_1^m, R, k) > F(R_2^m, R, k) + \Omega$ whenever $N(R_1^m, k)/N(R, k) < b$ and (2) $F(R_2^m, R, k) > F(R_1^m, R, k) + \Omega$ whenever $N(R_1^m, k)/N(R, k) > b$, then one of the following holds: (1) there exists a j such that $R_1^m(j) = \emptyset$; (2) there exists a j such that $R_2^m(j) = \emptyset$; or (3) for any number M there exists j' and j" such that $j' \geq M$, $j'' \geq M$, $N(R_1^m, j')/N(R, j') \leq b$, and $N(R_1^m, j'')/N(R, j'') \geq b$.

Section 4.6: Hereditary Variation

The next constituent of Darwin's theory that will be stated as an axiom is:(22)

> "it would be a most extraordinary fact that if no variations had ever occurred useful to each beings own welfare....if variations useful to any organic being ever do occur,...from the strong principle of inheritance, these will tend to produce offspring similarly characterized".

now it may seemthat this ought to be translated into two axioms; one axiom stating that useful variations occur and the other stating the strong principle of inheritance. However, since variations that are not hereditary do occur, we cannot state (1) useful variations occur and (2) all variations are hereditary (from which two statements we could derive the statement that useful hereditary variations occur). Similarly, since some variations are not useful, we cannot state (1) some variations are hereditary and (2) all variations are useful (from which two statements we could also derive that useful hereditary variations occur). So if we want to state, without grossly misrepresenting the universe, that useful hereditary variations occur, we must state it as an axiom.

Axiom 4.4: (Hereditary Variation): For any population R and any generation m such that $N(R,m) \geq 2$, there exists $H(m)$ contained in $R(m)$ and $\Omega > 0$ such that $R(m+1) \neq H^m(m+1)$ and, for any $k \geq m$ such that $R(k) \neq H^m(k)$, $F(H^m,R,k) > F(R-H^m,R,k) + \Omega$.

Notation: The letter H will hereafter be used to denote the subpopulation guaranteed by this axiom.

This axiom states that in every generation m any population R contains a subset $H(m)$ which is superior to the remainder of the population in generation m and whose descendants are superior to the remainder of the population for as long as the population contains any organisms which are not descendants of $H(m)$.

Notice that $R(m+1) \neq H^m(m+1)$ implies that $R(m) \neq H(m)$. Therefore this stipulation means that there are at least two generations (m and $m+1$) for which $F(H^m,R,k) > F(R-H^m,R,k)+\Omega$. The fact that the subpopulation has the property of being better than the remainder of the population for as long as it is distinguishable means that the property (or whatever causes the property) is hereditary; the fact that it is distinguishable for at least two generations guarantees that the hereditary property is not fulfilled vacuously. (It would be fulfilled vacuously by, e.g., a subset $R_1(m)$ containing all organisms in $R(m)$ which have descendants; clearly $R_1^m(m+1) = R(m+1)$ so that, although R_1^m fulfills "for any $k \geq m$ such that $R(k) \neq R_1^m(k)$, $F(R_1^m,R,k) > F(R-R_1^m,R,k)+\Omega$," there is no inheritance of fitness since there is only one generation involved.

Notice that the hereditary variation axiom ~~guarantees~~ assumes not only that in at least some cases organisms inherit characteristics of their parents, but also that the environment of the organisms inherits characteristics of the environment of the organisms' parents, for fitness is the result of both the characteristics of the organism and the characteristics of the environment. For natural selection to work it is necessary that the environment be reasonably stable; i.e. that it be stable with respect to the characteristics for which the population is selected for long enough to force the population to change. Thus this axiom, which states that fitness is inherited, is more relevant to natural selection than the laws of Mendelian heredity, which merely state that characteristics are inherited.

Note that the set $H(m)$ guaranteed to exist for $R(m)$ by this axiom may be the descendants of the subpopulation guaranteed to exist for $R(m-1)$. If $H^{m-1}(m+1) \neq R(m+1)$, then $H^{m-1}(m)$ is a subset of $R(m)$ which fulfills the axiom. This does not mean, however, that the axiom guarantees only one variant subpopulation in the course of all time, since theorem 4.9 guarantees that the descendants of $H^{m}(m)$ can coexist with non descendants for only a limited period of time. Therefore the superior subset guaranteed for $m' = t(H^{m},R)$ cannot be simply the set of all descendants in $R(m')$ of $H^{m}(m)$, since $H^{m}(m') = R(m')$. Thus this axiom guarantees that there is always variation, and the survival of the fittest axiom guarantees that any particular variation of the type guaranteed (i.e. variation whose fitness characteristic does not oscillate) can only remain variable in the population for a limited period.

Section 4.7: A Nested Sequence of Subpopulations that Take Over

The preceeding paragraph contains the germs of two theorems which will now be formally stated. The first simply states that there always exists a subset which is fated to take over in a finite number of generations.

Theorem 4.13: For any population R and generation n such that $N(R,n) \geq 2$, there exists a subset $R_1(n)$, such that $R_1(n) \neq R(n)$, and a generation j such that $R_1(j) = R(j)$.

Suppose that $N(R,k) \geq 2$ for all k. Then, since the hereditary variation axiom states that there is hereditary fitness variation in every generation of R, there must be a subset H(j) of R(j) which has, along with its descendants, an advantage over the rest of the population. H^j will, in time, eliminate its less fit cousins (either by extermination or interbreeding); suppose this happens by generation j2. Then there must exist a subset H(j2) of R(j2) which has an hereditary advantage over the rest of the population; H^{j2} will, in time, eliminate its less fit cousins. Clearly this process will go on forever, with superior subpopulations becoming noticeable as soon as the previous superior population completes its takeover. This is stated in the following theorem.

Theorem 4.14: For any population R such that there exists a generation n such that $N(R,k) \geq 2$ for all $k \geq n$, there exists a set of generations $\{j1, j2, j3, \ldots ji \ldots\}$ and a subset $H^{ji}(ji)$ of $R(ji)$ for each generation in the set such that $j1 < j2 < j3 < \ldots < ji < \ldots$, $H^{ji}(ji) \subsetneq H^{j(i-1)}(ji)$ for each generation ji in the set, and $R(k) = H^{ji}(k)$ for all $k \geq j(i+1)$.

Section 4.8: On the Use of Infinity

Now the reader should notice that the assumption, in the previous two theorems, that R(k) contains at least two organisms for every $k \geq n$ implies that the population never dies out. As it is entirely possible that all life will one day be exterminated by some cosmic catastrophe, it is possible that there do not exist any populations for which this assumption is true. It is necessary, therefore, to ask whether the hypotheses of these theorems are sufficiently close to being true of the universe in which we live for their conclusions to give the sort of phenomena that can be expected in our universe.

In almost every non-trivial application of mathematics to the real world the concept of infinity is a necessary element of the mathematics involved. Calculus, which was invented by Newton to express certain relationships among physical bodies, uses the concept of infinite subdivisibility; calculus is very useful even though matter is not infinitely subdivisible. Similarly statistics, which is used to describe finite sets of chance happenings, is defined in terms of infinite sets; in spite of this, the conclusions of statistics prove of practical value. Clearly in both these fields there are assumptions, without which the fields cannot be defined, which are not true in our universe; but they are sufficiently close to being true to allow these fields to be of practical use. Similarly we expect that the infinity which must be introduced in order to get interesting results will prove to be sufficiently true to allow this theory to be of practical value; the populations alive today, in which we are most interested, have probably existed for only a finite time period, but if that period is sufficiently large the theory should be sufficiently close.

Section 4.9: Theorems on the Structure of Subpopulations that Take Over

The next theorem should be taken as a warning that we cannot reason backward from the fact that a certain subpopulation takes over to the conclusion that it is fitter. It would not, of course, be desirable to have an axiom system which implies that the subpopulation that takes over is always the best one, since this is not a characteristic of the universe that we wish to describe.

<u>Theorem 4.15</u>: If $R_1(n)$ is a subset of $R(n)$ such that there exists $\Omega>0$ such that $F(R_1^n,R,k) > F(R-R_1^n,R,k)+\Omega$ for all $k \geq n$ such that $R(k) \neq R_1^n(k)$, and $R_2(n)$ is a subset of $R(n)$ such that $R_1(n)$ is a subset of $R_2(n)$, then there exists a generation j such that $R_2^n(j) = R(j)$.

This theorem asserts that if R_1^n is being selected for, then any subpopulation R_2^n which contains R_1^n will seem to be being selected for. For example, suppose that $R_3(n)$ consists of all those organisms that are fitter than the average but which left no j-descendants because of chance catastrophes. Then let $R_2(n) = R(n) - R_3(n)$. Clearly $F(R_2^n,R,n) < F(R-R_2^n,R,n)$, but in spite of this R_2^n will be seen to exterminate R_3^n and to take over R. Thus the axioms do not guarantee that every subpopulation which survives is fitter than every subpopulation which does not; they guarantee that some subpopulations which survive do so because they are fitter.

Theorem 4.10 has shown that if a population is composed of two non-interbreeding subpopulations one of which is consistently superior to the other, then the inferior subpopulation will be exterminated. But what happens in the case when neither subpopulation is consistently superior? In view of the continual supply of subpopulations which, according to Theorem 4.14, arise to take over any population, can such non-competitive subpopulations continue to exist? And if they can, how do they coexist with the competitive populations which are taking over? The following theorem will show the relationship between such non-competitive sub-populations and the competitive populations.

Theorem 4.16: If $R(0) = R_1(0) \cup R_2(0)$ and (1) R_1^0 and R_2^0 are non-interbreeding for $k \geq 0$, (2) $N(R_1^0, k) \geq 1$ for all $k \geq 0$, and (3) $N(R_2^0, k) \geq 1$ for all $k \geq 0$, then there exist subsets $\bar{R}_1^0(0) \subset R_1^0(0)$ and $\bar{R}_2^0(0) \subset R_2^0(0)$, at least one of which is a non-trivial subset, and a generation j such that $\bar{R}_1^0(j) = R_1^0(j)$ and $\bar{R}_2^0(j) = R_2^0(j)$.

Clearly neither R_1^0 nor R_2^0 is consistently superior to the other, since the fact that they are non-interbreeding implies that a consistently inferior one would be exterminated and, by conditions (2) and (3) both remain in existence. According to the theorem, what happens in this case is that the takeover subpopulation, which we know must exist, contains some members of $R_1^0(0)$ (namely $\bar{R}_1^0(0)$) and also some members of $R_2^0(0)$ (namely $\bar{R}_2^0(0)$). Each of these sub-subpopulations eliminates the remainder of its own subpopulation.

It is obvious that this theorem could be extended to show the same results if R consisted of any finite number (instead of just two) of non-interbreeding, non-competitive subpopulations. We see therefore that although the axioms guarantee that there is competition within each population, they do not guarantee free competition; that is, there is no guarantee that the population is homogenous with respect to competition. Thus our use of the word population is very much wider than the usual use of the word; many groups that are populations in our sense of the word are not populations in the usual sense. However, since any group that is a population in the usual sense is also a population in our sense, any statement that we make about populations will also be true for populations in the usual meaning of the word.

Section 4.10: Conclusions

In this chapter four axioms have been stated and some of their implications discussed. There are many other hypotheses about the process of evolution which could be stated as axioms; there could be an axiom asserting that heredity is Mendelian, or one asserting that variation arises from random mutations. These would add power to the theory, but they are not necessary for natural selection. We assert, however, that the four axioms that have been stated are necessary for natural selection. We assert further that they are sufficient to define natural selection. (These assertions cannot be proved since natural selection has never been explicitly defined.) We shall call such a universe a Darwinian Universe.

<u>Definition</u>: A Darwinian Universe is a Biological Universe, $(B, \rhd, =)$, a function f on B, and a set P of populations such that axioms 4.1 through 4.4 are true statements about them.

<u>Notation</u>: $(B, \rhd, =, f, P)$ denotes a Darwinian Universe.

CHAPTER 4: APPENDIX

A Darwinian Universe $(B, \rhd, =, f, P)$ is a Biological Universe $(B, \rhd, =)$, a function f on B and a set P of populations such that the following axioms hold:

Axiom: 4.1: For any R in P, R is a lineage in $(B, \rhd, =)$.

Axiom: 4.2: For any O in B, f(O) is a positive real number.

Definition 4.1:

$$F(O,R,k) = \frac{f(O)}{\sum_{O_i \text{ in } R(k)} f(O_i)} \qquad \text{if } O \text{ is in } R(k)$$

$$= \quad 0 \qquad \text{if } O \text{ is not in } R(k)$$

Definition 4.2: Let $R^*(k) = R'(k) \cap R(k)$. Then

$$F(R',R,k) = \sum_{O \text{ in } R'(k)} F(O,R,k) \frac{N(R,k)}{N(R^*,k)} \qquad \text{if } R^*(k) \neq \emptyset$$

$$= \quad 0 \qquad \text{if } R\ (k) = \emptyset$$

Definition 4.3: For any integers j_1 and j_2, a partition, $p(j_1,j_2)$, of j_1,j_2 is a set of pairs of integers such that:
(1) for any pair (k_1,k_2) in $p(j_1,j_2)$ either $k_1 = j_1$ or there exists exactly one pair (k_1',k_2') in $p(j_1,j_2)$ such that $k_2' = k_1$;
(2) for any pair (k_1,k_2) in $p(j_1,j_2)$ either $k_2 = j_2$ or there exists exactly one pair (k_1'',k_2'') in $p(j_1,j_2)$ such that $k_1'' = k_2$;
(3) there exists exactly one pair (k_1,k_2) in $p(j_1,j_2)$ such that $k_1 = j_1$;

(4) there exists exactly one pair (k_1,k_2) in $p(j_1,j_2)$ such that $k_2 = j_2$;

(5) for any pair (k_1,k_2) in $p(j_1,j_2)$ there exists no pair (k_1',k_2') in $p(j_1,j_2)$ such that $k_1' < k_1 < k_2'$ or $k_1' < k_2 < k_2'$;

(6) for any pair (k_1,k_2) in $p(j_1,j_2)$, $j_1 \leq k_1 < k_2 \leq j_2$.

Notation: Let $N(p(j_1,j_2))$ denote the number of pairs in the partition $p(j_1,j_2)$.

Axiom 4.3: (Survival of the Fittest): For any R in P, if $R_1^m(j_1) \subset R(j_1)$ and there exists an $\Omega > 0$ such that $F(R_1^m,R,k) > F(R-R_1^m,R,k) + \Omega$ Ω for all k in $[j_1,j_2]$, then if $\Omega(j_2-j_1) \geq 1$ there exists a partition $p(j_1,j_2)$ such that for every pair (k_1,k_2) in the partition

$$N(R_1^m,k_2) - N(R-R_1^m,k_2) > N(R_1^m,k_1) - N(R-R_1^m,k_1)$$

and $N(p(j_1,j_2)) \geq \Omega(j_2-j_1)$.

Axiom 4.4: (Hereditary Variation): For any R in P and any positive integer m such that $N(R,m) \geq 2$, there exists $H(m) \subset R(m)$ and $\Omega > 0$ such that $R(m+1) \neq H^m(m+1)$ and, for any $k \geq m$ such that $R(k) \neq H^m(k)$, $F(H^m,R,k) > F(R-H^m,R,k) + \Omega$.

Some theorems which can be proved using these axioms follow.

Theorem 4.1: For any O' in R(k), 0 F(O'R,k) 1.

Proof: Since O' is in R(k),

$$F(O',R,k) = \frac{f(O)}{\sum\limits_{O_i \text{ in } R(k)} f(O_i)}$$

by definition 4.1. By axiom 4.2, the numerator is a positive number and the denominator is a positive number. Therefore the ratio is positive; i.e. $F(O',R,k) > 0$.

Since O' is in $R(k)$,

$$\sum_{O_i \text{ in } R(k)} f(O_i) = f(O') + \sum_{O_i \text{ in } R(k)-O'} f(O_i) ;$$

so $F(O',R,k)$ is of the form $\frac{a}{a+b}$ where $a > 0$ and $b \geq 0$. Therefore $F(O',R,k) \leq 1$.

Theorem 4.2: $F(O',R,k) = 0$ if and only if O' is not in $R(k)$.

Proof: By definition 4.1, O' not in $R(k)$ implies $F(O',R,k) = 0$. By theorem 4.1, O' in $R(k)$ implies $F(O',R,k) > 0$; therefore $F(O',R,k) = 0$ implies O' not in $R(k)$.

Theorem 4.3: $F(R',R,k) = 0$ if and only if $R'(k) \cap R(k) = \emptyset$.

Proof: By definition 4.2, $F(R',R,k) = 0$ when $R'(k) \cap R(k) = \emptyset$. Now suppose $R'(k) \cap R(k) \neq \emptyset$. Then there exist an organism O' in $R'(k) \cap R(k)$. By theorem 4.1, $F(O',R,k) \neq 0$. Clearly $N(R,k) > 0$, and $N(R^*,k) > 0$. (Remember that $R^*(k) = R'(k) \cap R(k)$.) Therefore

$$F(R',R,k) = \left(\sum_{O_i \text{ in } R'(k)} F(O_i,R,k) \right) \frac{N(R,k)}{N(R^*,k)} > 0.$$

Therefore, since the assumption that $R'(k) \cap R(k) \neq \emptyset$ leads to the conclusion that $F(R',R,k) > 0$, $F(R',R,k) = 0$ implies that $R'(k) \cap R(k) = \emptyset$.

<u>Theorem 4.4</u>: If $R(k) \neq \emptyset$, then $F(R,R,k) = 1$.

Proof: Since $R(k) \neq \emptyset$, $R(k) \quad R(k) = R(k) \neq \emptyset$.

Therefore

$$F(E,R,k) = \left(\sum_{O_i \text{ in } R(k)} F(O_i,R,k) \right) \frac{N(R,k)}{N(R,k)}$$

$$= \sum_{O_i \text{ in } R(k)} F(O_i,R,k)$$

$$= \sum_{O_i \text{ in } R(k)} \left(\frac{f(O_i)}{\sum_{O_i \text{ in } R(k)} f(O_i)} \right)$$

$$= \frac{\sum_{O_i \text{ in } R(k)} f(O_i)}{\sum_{O_i \text{ in } R(k)} f(O_i)}$$

$$= 1$$

<u>Notation</u>: In $F(R-R',R,k)$, $R-R'$ denotes $R(k) - R'(k)$.

<u>Theorem 4.5</u>: Let R and R' be such that $\emptyset \neq R'(k) \cap R(k) \neq R(k)$. Then $F(R',R,k) > 1$ if and only if $F(R-R',R,k) < 1$.

Proof: Let $R''(k) = R(k) - R'(k)$, $R_1^*(k) = R''(k) \cap R(k)$, and $R_2^*(k) = R'(k) \cap R(k)$. Then

$$F(R-R',R,k) = F(R'',R,k)$$

$$= \frac{N(R,k)}{N(R_1^*,k)} \left(\sum_{O_i \text{ in } R''(k)} F(O_i,R,k) \right)$$

$$= \frac{N(R,k)}{N(R_1^*,k)} \left[1 - \sum_{O_i \text{ in } R'(k)} F(O_i,R,k) \right]$$

$$= \frac{N(R,k)}{N(R_1^*,k)} - \frac{N(R,k)}{N(R_1^*,k)} \left(\sum_{O_i \text{ in } R'(k)} F(O_i,R,k) \right)$$

$$= \frac{N(R,k)}{N(R_1^*,k)} - \frac{N(R_2^*,k)}{N(R_1^*,k)} \quad F(R',R,k)$$

$$\frac{N(R,k) - N(R,k)F(R',R,k) + N(R_1^*,k)F(R',R,k)}{N(R_1^*,k)}$$

$$= \frac{N(R,k)}{N(R_1^*,k)} \left[1 - F(R',R,k)\right] + F(R',R,k).$$

Now suppose $F(R',R,k) > 1$; then $F(R',R,k) = 1 + \delta$ for $\delta > 0$. Therefore

$$F(R-R',R,k) = \frac{N(R,k)}{N(R_1^*,k)} \left[1 - (1 + \delta)\right] + 1 + \delta$$

$$< 1 \quad \text{since} \quad \frac{N(R,k)}{N(R_1^*,k)} > 1.$$

On the other hand, suppose $F(R-R',R,k) < 1$; then $F(R-R',R,k) = 1 - \delta$.

So $$1 - \delta = \frac{N(R,k)}{N(R_1^*,k)} \left[1 - F(R',R,k)\right] + F(R',R,k)$$

If $F(R',R,k) \not> 1$, then either (1) $F(R',R,k) = 1$ or (2) $F(R',R,k) = 1 - \delta$.

If (1) then $1-\delta = \frac{N(R,k)}{N(R_1^*,k)} \cdot 0 + 1$, which is impossible.

If (2) then $1-\delta = \frac{N(R,k)}{N(R_1^*,k)} \left[1-(1-\delta)\right] + 1-\delta$

but since the right side of the equation is greater than 1, this is impossible. Therefore, since assuming $F(R',R,k) \not> 1$ leads to a contradiction, $F(R',R,k) > 1$.

Theorem 4.6: Let $R'(k)$ be a non-trivial subset of $R(k)$. Then $F(R',R,k) = 1$ if and only if $F(R-R',R,k) = 1$.

Proof: Only if: Assume the contrary; i.e. $F(R',R,k) = 1$ and $F(R-R',R,k) \neq 1$. Then either (1) $F(R-R',R,k) < 1$ or (2) $F(R-R',R,k) > 1$. By theorem 4.5, $F(R-R',R,k) < 1$ implies $F(R',R,k) > 1$; therefore $F(R',R,k)$ cannot be equal to 1 when $F(R-R',R,k) < 1$; therefore (1) cannot be true. Let $R_1(k) = R(k) - R'(k)$; then $R(k) - R_1(k) = R (k)$. Now using theorem 4.5 on $R_1(k)$, $F(R_1,R,k) > 1$ implies that $F(R-R_1,R,k) < 1$; substituting equal sets, this implies that $F(R-R',R,k) > 1$ implies $F(R',R,k) < 1$; therefore (2) cannot be true. Since neither (1) nor (2) can be true, it cannot be true that $F(R',R,k) = 1$ and $F(R-R',R,k) \neq 1$.

If: The proof of the implication in the other direction is analogous.

Theorem 4.7: Let $R'(k)$ be a non-trivial subset of $R(k)$. Then $F(R',R,k) > F(R,R,k)$ if and only if $F(R',R,k) > F(R-R',R,k)$.

Proof: If: By theorem 4.4, $F(R,R,k) = 1$; therefore $F(R',R,k) > F(R,R,k)$ implies $F(R',R,k) > 1$. This implies, by theorem 4.5, $F(R-R',R,k) < 1$. Therefore $F(R',R,k) > F(R-R',R,k)$.

Only if: Assume the contrary: i.e. (1) $F(R',R,k) > F(R-R',R,k)$ and (2) $F(R',R,k) \leq 1$. But by theorem 4.6, $F(R',R,k) = 1$ implies $F(R-R',R,k) = 1$ and by theorem 4.5 $F(R',R,k) < 1$ implies $F(R-R',R,k) > 1$. Thus statements (1) and (2) cannot both be true. Therefore $F(R',R,k) > F(R-R',R,k)$ implies $F(R',R,k) > 1 = F(R,R,k)$.

Theorem 4.8: For any integer i such that $j_1 \leq i \leq j_2$ and for any partition $p(j_1,j_2)$, there exists a pair (k_1,k_2) in $p(j_1,j_2)$ such that $k_1 \leq i \leq k_2$.

Proof: Suppose that no such (k_1,k_2) exists. By the definition there exists a (k_1,k_2) such that $k_1 = j_1$; therefore, since $i \geq j_1$, there exists at least one (k_1,k_2) such that $k_1 \leq i$. Since there are a finite number of pairs in the partition, they are well-ordered; therefore there exists a pair (k_1'',k_2'') such that k_1'' is the largest k_1 less than i. By part (2) of the definition, either $k_2'' = j_2$ or there exists (k_1',k_2') such that $k_1' = k_2''$. But by the assumption $i \not\leq k_2''$; therefore $i > k_2''$. This implies that either k_1'' is not the largest k_1 less than i, which is impossible, or $i > j_2$, which is impossible. Therefore, since the assumption that no such (k_1,k_2) exists leads to a contradiction, such a pair must exist.

Lemma 4.9: For any population R and integer m there exist no $R_1^m(m) \subset R(m)$ such that there exists $\Omega > 0$ and k' such that $F(R_1^m, R, k) > F(R-R_1^m, R, k) + \Omega > \Omega$ for all $k \geq k'$.

Proof: Suppose such an $R_1^m(m)$ exists. Let $i_1 = k'$. Since Ω is a constant, there exists an integer i_2 such that $\Omega(i_2-i_1) \geq 1$. Therefore, by the survival of the fittest axiom, there exists a partition $p(i_1,i_2)$ such that $N(p(i_1,i_2)) \geq 1$ and for every $k_1,k_2)$ in the partition

$$N(R_1^m,k_2) - N(R-R_1^m,k_2) > N(R_1^m,k_1) - N(R-R_1^m,k_1).$$

Again, since Ω is a constant, there exists an integer i_3 such that $\Omega(i_3-i_2) \geq 1$. Therefore, by the survival of the fittest axiom there exists a partition $p(i_2,i_3)$ such that $N(p(i_2,i_3)) \geq 1$ and for every (k_1,k_2) in the partition

$$N(R_1^m,k_2) - N(R-R_1^m,k_2) > N(R_1^m,k_1) - N(R-R_1^m,k_1).$$

Similarly there exist an infinite succession of integers $i_4, i_5, i_6, \ldots$ with the same properties.

Let $S(R,R_1^m,k_1,k_2) = [N(R_1^m,k_2)-N(R-R_1^m,k_2)] - [N(R_1^m,k_1)-N(R-R_1^m,k_1)]$.

Then, by the survival of the fittest axiom,

$$\sum_{j=1}^{3M_R} N(p(i_j,i_{j+1})) \leq \sum_{j=1}^{3M_R} \left(\sum_{\substack{(k_1,k_2) \text{ in} \\ p(i_j,i_{j+1})}} S(R,R_1^m,k_1,k_2) \right) \quad (1)$$

Now since, in a partition, every k_1 except the first is equal to the k_2 of the next smaller pair and every k_2 except the last is equal to the k_1 of the next larger pair, the inner sum on the right side of (1) is of the form

$$(a-b)+(b-c)+(c-d)+\dots+(x-y)+(y-z) = a-z$$

So the right side reduces to

$$\sum_{j=1}^{3M_R} \left\{ \left[N(R_1^m, i_{j+1}) - N(R-R_1^m, i_{j+1})\right] - \left[N(R_1^m, i_j) - N(R-R_1^m, i_j)\right] \right\}.$$

But this is clearly of the same form, so it reduces to

$$\left[N(R_1^m, i_{3M_R}) - N(R-R_1^m, i_{3M_R})\right] - \left[N(R_1^m, i_1) - N(R-R_1^m, i_1)\right].$$

Now since each member of the sum on the left of (1) is at least 1,

$$3M_R \leq \sum_{j=1}^{3M_R} N(p(i_j, i_{j+1})).$$

So, according to (1),

$$3M_R \leq \left[N(R_1^m, i_{3M_R}) - N(R-R_1^m, i_{3M_R})\right] - \left[N(R_1^m, i_1) - N(R-R_1^m, i_1)\right]. \quad (2)$$

Now, since $N(R', k) \geq 0$, (2) implies

$$3M_R \leq N(R_1^m, i_{3M_R}) + N(R-R_1^m, i_1) \quad (3)$$

But by axiom 3.4, $N(R, k) \leq M_R$, so (3) implies

$$3M_R \leq 2M_R.$$

This is clearly impossible. By assuming that such an R_1^m exists we have shown that this gives rise to a contradiction. Therefore no such R_1^m exists.

<u>Theorem 4.9</u>: If $R_1(m) \subseteq R(m)$ and there exists an $\Omega > 0$ such that $F(R_1^m, R, k) > F(R - R_1^m, R, k) + \Omega$ for all k such that $k \geq m$ and $R_1^m(k) \neq R(k)$, then there exists an integer t such that $R(t) = R_1^m(t)$.

Proof: Suppose no such t exists. If we let $R_2(k) = R(k) - R_1^m(k)$, then this assumption asserts that $R_2(k) \neq \emptyset$ for any $k \geq m$. Therefore, $R_2(k) \cap R(k) \neq \emptyset$ for any $k \geq m$, so by theorems 4.3 and 4.1, $F(R_2, R, k) > 0$ for any $k \geq m$. Therefore, for any $k \geq m$, $F(R_2, R, k) + \Omega > \Omega$. Therefore $F(R_1^m, R, k) > F(R - R_1^m, R, k) + \Omega > \Omega$ for all $k > m$. But by lemma 4.9 this is impossible. Therefore such a t must exist.

<u>Notation:</u> If R_1^m is a subpopulation of R which fulfills the conditions of theorem 4.9 and t is the generation guaranteed by the theorem, then we shall call t the takeover generation of R_1^m with respect to R and we shall denote it by $t(R_1^m, R)$.

<u>Definition 4.4</u>: R_1^{j1} and R_2^{j2} are non-interbreeding for $i \geq k$ if and only if $R_1^{j1}(i) \cap R_2^{j2}(i) = \emptyset$ for $i \geq k$.

<u>Theorem 4.10</u>: If $R(k) = R_1^m(k) \quad R_2^m(k)$, $R_1^m(k)$ and $R_2^m(k)$ are non-interbreeding for $k \geq m$, and there exists $\Omega > 0$ such that $F(R_1^m, R, k) > F(R_2^m, R, k) + \Omega$ for all k such that $k \geq m$ and $R_1^m(k) \neq R(k)$, then $R_2^m(t(R_1^m, R)) = \emptyset$.

Proof: R_1^m satisfies the conditions of theorem 4.9. Therefore $R_1^m(t(R_1^m,R)) = R(t(R_1^m,R))$. Since $R_2^m(k) \subset R(k)$ for all k, this implies that $R_2^m(t(R_1^m,R)) \subset R_1^m(t(R_1^m,R))$. But since R_1^m and R_2^m are non-interbreeding for $k \geq m$ and $t(R_1^m,R) > m$, $R_1^m(t(R_1^m,R)) \cap R_2^m(t(R_1^m,R)) = \emptyset$. Therefore $R_2^m(t(R_1^m,R)) = \emptyset$.

<u>Theorem 4.11</u>: If there exists an $\Omega > 0$ and a number b such that $F(R_1^m,R,k) > F(R-R_1^m,R,k) + \Omega$ for all k such that $N(R_1^m,k)/N(R,k) \leq b$, then there exists an integer j such that $N(R_1^m,j)/N(R,j) \geq b$.

Proof: Suppose that no such j exists. Then $F(R_1^m,R,k) > F(R-R_1^m,R,k) + \Omega$ Ω for all k. But by lemma 4.9 this is impossible. Therefore such a j must exist.

<u>Theorem 4.12</u>: If $R(k) = R_1^m(k) \cup R_2^m(k)$ for all $k \geq m$, R_1^m and R_2^m are non-interbreeding for all $k \geq m$, and there exist numbers b and $\Omega > 0$ such that (1) $F(R_1^m,R,k) > F(R_2^m,R,k) + \Omega$ whenever $N(R_1^m,k)/N(R,k) < b$ and (2) $F(R_2^m,R,k) > F(R_1^m,R,k) + \Omega$ whenever $N(R_1^m,k)/N(R,k) > b$, then one of the following holds: (1) there exists a j such that $R_1^m(j) = \emptyset$; (2) there exists a j such that $R_2^m(j) = \emptyset$; or (3) for any number M there exist j' and j" such that $j' \geq M$, $j'' \geq M$, $N(R_1^m,j')/N(R,j') \leq b$, and $N(R_1^m,j'')/N(R,j'') \geq b$.

Proof: Suppose neither (1) nor (2) holds and there does not exist such a j". Then for all $k \geq M$, $N(R_1^m,k)/N(R,k) < b$, which implies that $F(R_2^m,R,k) > F(R_1^m,R,k) + \Omega$. Since (1) does not hold, theorems 4.1 and 4.3 imply that $F(R_1^m,R,k) > 0$. Therefore, since R_1^m and R_2^m non-interbreeding implies that $R_1^m(k) = R(k) - R_2^m(k)$, $F(R_2^m,R,k) > F(R-R_2^m,R,k) + \Omega > \Omega$ for all $k \geq M$. But this is impossible by lemma 4.9, so we have arrived at a contradiction. Therefore such a j'' must exist.

Suppose neither (1) nor (2) holds and there does not exist such a j'. Then for all $k \geq M$, $N(R_1^m,k)/N(R,k) > b$, which implies that $F(R_1^m,R,k) > F(R_2^m,R,k) + \Omega$. Since (2) does not hold, theorems 4.1 and 4.3 imply that $F(R_2^m,R,k) > 0$. Therefore, since R_1^m and R_2^m non-interbreeding implies that $R_2^m(k) = R(k) - R_1^m(k)$, $F(R_1^m,R,k) > F(R-R_1^m,R,k) + \Omega > \Omega$ for all $k \geq M$. But this is impossible by lemma 4.9, so we have arrived at a contradiction. Therefore such a j' must exist.

Theorem 4.13: For any R in P and any n such that $N(R,n) \geq 2$, there exists $R_1(n) \subset R(n)$ such that $R_1(n) \neq R(n)$ and a generation j such that $R_1^n(j) = R(j)$.

Proof: The hereditary variation axiom guarantees that there exists an $H(n) \subsetneq R(n)$ such that $H(n) \neq R(n)$ and, for any $k \geq n$ such that $R(k) \neq H^n(k)$, $F(H^n,R,k) > F(R-H^n,R,k) + \Omega$. Let $R_1(n) = H(n)$. Then $R_1(n) \subsetneq R(n)$; we must now prove that there exists a j such that $R_1^n(j) = R(j)$. Suppose there exists no such j. Then $R(k) - R_1^n(k) \neq \emptyset$ for any $k \geq n$; so by theorems 4.1 and 4.3, $F(R-R_1^n,R,k) > 0$ for all $k \geq n$.

Therefore $F(R^n_1,R,k) > F(R-R^n_1,R,k) + \Omega > \Omega$ for all $k \geq n$. But, by lemma 4.9, this is impossible, so we have arrived at a contradiction by assuming that no such j exists. Therefore such a j must exist.

Theorem 4.14: For any R in P such that there exists a generation n such that $N(R,k) \geq 2$ for all $k \geq n$, there exists a set of generations $\{j1,j2,j3,\ldots\}$ and a subset $H^{ji}(ji) \subsetneq R(ji)$ for each generation in the set such that (1) $j1 < j2 < j3 < \ldots$, (2) $H^{ji}(ji) \subsetneq H^{j(i-1)}(ji)$ for each generation in the set, and (3) $R(k) = H^{ji}(k)$ for all $k \geq j(i+1)$.

Proof: We shall prove this by mathematical induction. First we must show that there exists $j1, j2, H^{j1}, H^{j2}$ such that $H^{j1}(j2) \supsetneq H^{j2}(j2)$ and $R(k) = H^{j1}(k)$ for all $k \geq j2$. Since $N(R,k) \geq 2$ for all $k \geq n$, there exists, by theorem 4.13, a subset $H(n) \subsetneq R(n)$ and an integer $j > n$ such that $H^n(j) = R(j)$. By theorem 3.4, $H^n(j) = R(j)$ implies that $H^n(k) = R(k)$ for all $k \geq j$. Therefore, if we let $j1 = n$, $j2 = j$, and $H^{j1}(j1) = H^n(n)$, then $H^{j1}(j1) \subsetneq R(j1)$ and $H^{j1}(k) = R(k)$ for all $k \geq j2$.

Now we can apply theorem 4.13 again, letting $m = j2$. Therefore there exist a subset $H(j2) \subsetneq R(j2)$ and an integer $j > j2$ such that $H^{j2}(j) = R(j)$, and thus $H^{j2}(k) = R(k)$ for all $k \geq j$. Letting $j3 = j$, we have $H^{j2}(k) = R(k)$ for all $k \geq j3$. Since $H^{j1}(j2) = R(j2)$, $H^{j2}(j2) \subsetneq H^{j1}(j2)$.

Now we must show that if (1) there exist ji, $j(i+1)$, $j(i+2)$, H^{ji}, and $H^{j(i+1)}$ such that $H^{j(i+1)}(j(i+1)) \subsetneq H^{ji}(j(i+1))$ and $R(k) = H^{j(i+1)}(k)$ for all $k \geq j(i+2)$ then there exist $j(i+3)$ and $H^{j(i+2)}$ such that $H^{j(i+2)}(j(i+2)) \subsetneq H^{j(i+1)}(j(i+2))$ and $R(k) = H^{j(i+2)}(k)$ for all $k \geq j(i+3)$. We apply theorem 4.13, letting $m = j(i+2)$; thus there exist $H(j(i+2)) \subsetneq R(j(i+2))$ and an integer $j > j(i+2)$ such that $H^{j(i+2)}(j) = R(j)$. Letting $j(i+3) = j$, we have that $H^{j(i+2)}(j(i+3)) = R(j(i+3))$ and therefore, by theorem 3.4, that $H^{j(i+2)}(k) = R(k)$ for all $k \geq j(i+3)$. Since $H^{j(i+1)}(j(i+2)) = R(j(i+2))$, $H^{j(i+2)}(j(i+2)) \quad H^{j(i+1)}(j(i+2))$. This completes the proof by induction.

<u>Theorem 4.15</u>: If $R_1(n) \subset R(n)$ and there exists $\Omega > 0$ such that $F(R_1^n, R, k) > F(R - R_1^n, R, k) + \Omega$ for all $k \geq n$ such that $R(k) \neq R_1^n(k)$, and there exists $R_2(n)$ such that $R_1(n) \subset R_2(n) \subset R(n)$, then there exists a generation j such that $R_2^n(j) = R(j)$.

Proof: By theorem 4.9, there exists a j such that $R_1^n(j) = R(j)$. By theorem 3.3, $R_1^n(n) \subset R_2^n(n) \subset R(n)$ implies that $R_1^n(j) \subset R_2^n(j) \subset R(j)$. Then $R(j) = R_1^n(j) \subset R_2^n(j) \subset R(j)$ implies $R_2^n(j) = R(j)$.

<u>Theorem 4.16:</u> If $R(0) = R_1(0) \cup R_2(0)$ and (1) R_1^0 and R_2^0 are non-interbreeding for $k \geq 0$, (2) $N(R_1^0, k) \quad 1$ for all $k \geq 0$, and (3) $N(R_2^0, k) \geq 1$ for all $k \geq 0$, then there exist non-null subsets $\bar{R}_1^0(0) \subset R_1^0(0)$ and $\bar{R}_2^0(0) \subset R_2^0(0)$, at least one of which is a non-trivial subset, and a generation j such that $\bar{R}_1^0(j) = R_1^0(j)$ and $\bar{R}_2^0(j) = R_2^0(j)$.

Proof: By theorem 4.13 there exists a subset $H(0) \subsetneq R(0)$ and a generation j such that $H^0(j) = R(j)$. Now there are three possibilities: (a) $H^0(j) \subset R_1^0(j)$; (b) $H^0(j) \subset R_1^0(j)$, and (c) $H^0(j) \cap R_1^0(j) \neq \emptyset$ and $H^0(j) \cap R_1^0(j) \neq \emptyset$.

Suppose (a) is true. Since R_1^0 and R_2^0 are non-interbreeding, $R_1^0(j) \cap R_2^0(j) = \emptyset$, which implies that $R(j) \cap R_2^0(j) = \emptyset$. But this implies that $R_2^0(j) = \emptyset$, which is impossible by part (3) of the hypothesis. Therefore (2) is not true.

(b) can be shown to be false by the same argument.

Therefore (c) is true. This implies, by the definition of R, that $H^0(0) \cap R_1^0(0)$ and $H^0(0) \cap R_1^0(0)$ are the subsets required.

CHAPTER 5: DIVERSE DARWINIAN UNIVERSES

Having delineated the process of natural selection, we now wish to indicate how this process, together with the diversity of environments, acts to produce the diversity of species. We shall not give a set of axioms which are necessary and sufficient to produce diversity of species, for this is too complex a problem to be completely solved here. The purpose of this chapter is, rather, to indicate how the theory of the Darwinian Universe can be embedded in a larger theory in which the production of diversity by natural selection can be discussed. This will be done by embedding the Darwinian Universe in a system, called a Diverse Darwinian Universe, in which the existence of environments with different selective effects is postulated.

Section 5.1: Environments

We shall not actually discuss environments; we shall confine the discussion to different fitness functions for the same set of organisms and their different selective effects. However, since the concept of different environments which have different effects on the same set of organisms is what gives rise to the concept of different fitness functions and since the properties that we give to the fitness functions are intuitively derived from the properties that we see in environments, we shall first give an intuitive discussion of the concept of environment which will form a background to the properties of fitness functions.

Intuitively, the environment of an organism is the set of all factors which influence its life, including both physical factors (climate, soil type, etc.) and biological factors (predators, parasites, food, etc.). Thus the environment of the organism is not wholly determined by its surroundings; it is partly determined by the capabilities of the organism. For example, the colour red is not part of the environment of a colour blind organism; the organism may be more likely to be caught by a predator if seen against a red background, but this will not make red a selective factor ~~unless~~ if the organism has ~~some~~ no way of differentiating between red and not-red, since there is nothing in a population of such organisms to select for. Thus the environment of a population, which may be thought of as the "sum" of the environments of the individual organisms comprising it, may be changed either by changes internal to the organisms or by changes external to the organisms.

Within a Diverse Darwinian Universe we shall be able to discuss such changes and to differentiate between internal and external changes. We shall do this by considering the fitness in an environment α of an organism O, given by $f_\alpha(O)$, and the fitness in environment β of the same organism O, given by $f_\beta(O)$. (Except for the letter Ω, all of the Greek letters used hereafter will denote environments; Ω will be used, as before, to denote a small positive number.) We shall stipulate that each environment α (or β, γ, etc.) is a Darwinian Universe with fitness function f_α (or f_β, f_γ, etc.); that is, the function f_α on the Biological Universe $(B, \not\triangleright, =)$ has the properties ascribed to the function f by axioms 4.1 through 4.4. The set of such functions will be denoted by E as a reminder of its connection with environments.

Notice that if the fitness function f_α is different from the fitness function f_β (i.e. f_α and f_β select for different properties), then, under natural selection, the population derived by f_α from a given set S of organisms will be different from the population derived by f_β from S; thus we designate a population in α by R_α and the population in β by R_β; similarly we designate by P_α and P_β the sets of populations in α and β. The first axiom simply states that every f_α in E is a Darwinian fitness function.

<u>Axiom 5.1</u>: For any f_α in E, $(B, \not\triangleright, =, f_\alpha, P_\alpha)$ is a Darwinian Universe.

The stipulation that each environment gives rise to a Darwinian Universe automatically excludes the possibility of emigration into an environment at a rate sufficiently high to upset the Darwinian properties. For example, suppose we wish to study a population R on the edge of the range of its species and which is such that (1) at all times a certain subset R' is more fit than its complement R-R' in the situation in which both are living but (2) R-R' actually has an advantage over R' because of emigration from the interior of the range of the species; this "population" R cannot be studied by itself (i.e. without reference to the emigrants' parent population and its environment), since the Darwinian properties will not hold if f_α is interpreted to mean fitness in the immediate environment of R; in this case it is necessary to consider the environment of the whole of the population which is contributing descendants to R. (Biologists will recognize that this is related to the problem of the effect of reproductive isolation on selection.) On the other hand, the axiom does not exclude emigration which can be absorbed without upsetting the Darwinian properties.

Section 5.2: Equivalent Subpopulations

It is intuitively clear that a subpopulation which is more fit than its complement in one environment may be less fit than its complement in another environment. (For example, giraffes with long necks may be more fit than giraffes with short necks in an environment containing tall trees, but less fit than giraffes with short necks in an environment containing only low bushes.) We could denote this situation by: $F_\alpha(R_1,R,k) > F_\alpha(R-R_1,R,k)$ but $F_\beta(R_1,R,k) < F_\beta(R-R_1,R,)$. However, this statement of the situation assumes that the same organisms are present in both environments. This, while intuitively clear, is physically impossible, since the fitness assigned to an organism by the fitness function is its fitness over its whole lifetime. Now, if an organism moves from α to β its fitness may be given by f_γ, where the environment γ is a combination of the environments α and β, but f_γ is not a simple combination of f_α and f_β since the fact that the organism has spent part of its life in α will influence its reaction to β. With such a concept of fitness, how can we explicitly state the intuitively clear fact that there exist populations and environments such that one subpopulation will be selected for in one environment while its complement will be selected for in another environment?

In order to do this it will be necessary to introduce the concept of equivalent subsets. Roughly speaking, a subset S' of S and its complement S-S' are equivalent to each other with respect to a subset D of S if the organisms in D are randomly (with respect to fitness) divided between S and S-S'. Thus, for two such equivalent subsets,

$F_\alpha(D\cap S',\ S',0) > 1$ when and only when $F_\alpha(D\cap(S-S'),S-S',0)>1$. Now this relationship between fitnesses is the property that equivalent sets must have in order to provide a tool for discussing the different selective effects of different environments; with it we can say that if $F_\alpha(D\cap S',S',0) > 1$ and $F_\beta(D\cap(S-S'),S-S',0)<1$ then α and β are different environments. This relationship is not, however, a property of randomly divided subsets; random division does not always ensure fair division; it only ensures that on the average the division will be fair. We shall, therefore, define equivalent subsets not in terms of random division but in terms of the relationship between fitnesses.

But first, in order to express this and succeeding concepts somewhat more concisely, it is desirable to define a notation for certain sets which will appear in definition 5.1, axiom 5.2, and some of the theorems in this chapter.

<u>Notation</u>: Given f_α in E and sets S, $S'\subset S$, and $D\subset S$, the following notation will be used for the indicated subsets:

(1) $S^* = S-S'$

(2) $R'_\alpha(0) = S'$

(3) $R^*_\alpha(0) = S$

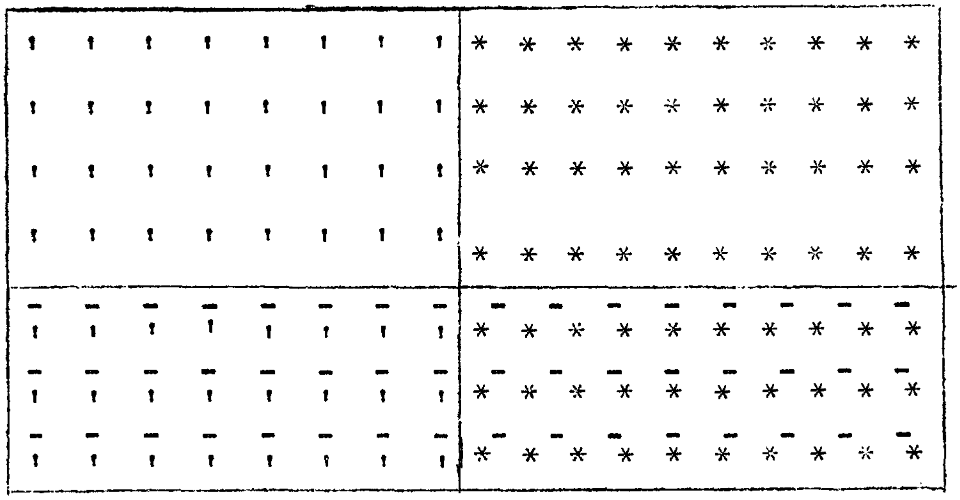
(4) $D'_\alpha(0) = D\cap S'$

(5) $D^*_\alpha(0) = D\cap S^*$

(6) $\bar{D}'_\alpha(0) = S' - D\cap S'$

(7) $\bar{D}^*_\alpha(0) = S^* - D\cap S^*$

A visual representation of the sets mentioned in this notation is provided by the following diagram.



The whole figure represents the set S. The right hand rectangle, containing the symbol *, represents S^*. The left hand rectangle, containing the symbol ', represents S'. (Notice that $S^* = S-S'$). The bottom rectangle, containing the symbol -, represents D. (The fact that the areas of the different rectangles are approximately equal should not be taken to mean that all of the subsets contain the same numbers of organisms.) The set $D \cap S'$ is the part of the figure containing both - and '. The set $D \cap S^*$ is the part of the figure containing both - and *.

<u>Definition 5.1</u>: A set $S' \subset S \subset B$ is equivalent in generation k to S with respect to $D \subset S$ and f_α in $\mathbb{E}$ if and only if for any R'_α in P_α and for any R^*_α in P_α, when (a) designates the inequality

$$F_\alpha(D'^0_\alpha, R'_\alpha, k) > F_\alpha(R'_\alpha - D'^0_\alpha, R'_\alpha, k) + \Omega \qquad (a)$$

and (b) designates the inequality

$$F_\alpha(D^{*0}_\alpha, R^*_\alpha, k) > F_\alpha(R^*_\alpha - D^{*0}_\alpha, R^*_\alpha, k) + \Omega \qquad (b)$$

Then for any $\Omega > 0$ (a) $\Longleftrightarrow$ (b).

To illustrate this definition, consider the example of the giraffes. Suppose the environment α is such that the longer the giraffe's neck, the greater its fitness. Then if S is the set of giraffes in α, let D be the set of all giraffes in α with necks longer than a fixed length x; then S-D is the set of all giraffes in α with necks shorter than or equal to the length x. Assume that there are exactly 100 giraffes in S. Let the giraffes in S be numbered so that g_1 has the longest neck, g_2 has the second longest neck, and in general g_i has a longer neck than g_{i+1}. Then $D = \{g_1, g_2, \ldots, g_m\}$ and $S-D = \{g_{m\ 1}, g_{m\ 2}, \ldots, g_{100}\}$. Let S' be the subset

$$S' = R'_\alpha(0) = \{g_1, g_3, g_5, \ldots, g_{m\ 1}, g_{m\ 3}, \ldots, g_{99}\}$$

Then $$S^* = R^*_\alpha(0) = \{g_2, g_4, g_6, \ldots, g_m, g_{m\ 2}, \ldots, g_{100}\}$$

$$D'_\alpha(0) = \{g_1, g_3, g_5, \ldots, g_p\} \quad \text{where } p = m \text{ or } p = m - 1$$

$$D^*_\alpha(0) = \{g_2, g_4, g_6, \ldots, g_q\} \quad \text{where } q = m \text{ or } q = m - 1$$

From the way S' and S* are defined it is clear that they have approximately equal relative fitnesses with respect to D; i.e., if $F_{\alpha}(D'^{0}_{\alpha}, R'_{\alpha}, 0) > F(R'_{\alpha} - D'^{0}_{\alpha}, R'_{\alpha}, 0)$ then $F_{\alpha}(D^{*0}_{\alpha}, R^{*}_{\alpha}, 0) > F_{\alpha}(R^{*}_{\alpha} - D^{*0}_{\alpha}, R^{*}_{\alpha}, 0)$ or, to put this in words, if in α the fitness of that part of D which is in S' is greater than the fitness of its complement in S', then the fitness of that part of D which is in S* is greater than the fitness of its complement in S*.

In this example S' and S* were formed so that they had approximately equal numbers of giraffes from D and so that the number of giraffes in S' was approximately equal to the number of giraffes in S*. Neither of these conditions are necessary for equivalent sets. The necessary condition is the one stipulated in the definition, namely that the relation between the fitnesses of D' and S'-D' is the same as that between the fitnesses of D* and S* -D*. These relations could be the same even if S' contained only a small fraction of the giraffes in S; therefore a small set of giraffes which is separated from its parent population by an earthquake may be equivalent to its parent population with respect to D even though it is very much smaller than its parent population.

So far we have only considered the situation when S' and S* are equivalent in one generation. Because length of neck, and therefore fitness due to length of neck, is hereditary we would expect that if the fitness of D' is greater than that of R'-D' in the zeroth generation, then it will be greater in the first generation; i.e. if $F_\alpha(D_\alpha'^0, R_\alpha', 0) > F_\alpha(R_\alpha' - D_\alpha'^0, R_\alpha', 0)$ then $F_\alpha(D_\alpha'^0, R_\alpha', 1) > F_\alpha(R_\alpha' - D_\alpha'^0, R_\alpha', 1)$. In fact, if S' is well chosen, we could expect that the fitness of D' is greater in the kth generation, for k any positive integer. (Remember that if $D_\alpha'^0$ takes over R_α' by generation j then $1 = F_\alpha(D_\alpha'^0, R_\alpha', k) > F_\alpha(R_\alpha' - D_\alpha'^0, R_\alpha', k) = 0$ for all $k \geq j$.) This is the kind of set we are most interested in, since we would like to compare the effect of natural selection on two sets S' and S which are equivalent with respect to D in environment α over many generations and are also equivalent with respect to D in environment β over many generations. If S' and S* are such sets then we can consider the effect of natural selection on S' in environment α and on S* in environment β and know that differences in the resulting populations in the kth generation would be due to differences in α and β rather than to differences in S' and S*.

Axiom 5.2: For any f_α in E and any R_α in P_α, there exists an m such that if $S = R_\alpha(m)$, then there exists $S' \subset S$, $D \subset S$, f_β in E, and Ω 0 such that

(1) $N(R_\alpha, m) > 0$

(2) $R_\alpha'^m$ is equivalent in all $k \geq m$ to R_α^{*m} with respect to D and f_α

(3) R'^{m}_{β} is equivalent in all $k \geq m$ to R^{*m}_{β} with respect to D and f_{β}.

(4) $F_{\alpha}(D'^{0}_{\alpha}, R'_{\alpha}, k) > F_{\alpha}(R'_{\alpha} - D'^{0}_{\alpha}, R'_{\alpha}, k) + \Omega$ for any $k \geq m$ such that $R'_{\alpha}(k) \neq 0$.

(5) $F_{\beta}(D'^{0}_{\beta}, R'_{\beta}, k) > F_{\beta}(R'_{\beta} - D'^{0}_{\beta}, R'_{\beta}, k) + \Omega$ for any $k \geq m$ such that $R'_{\beta}(k) \neq 0$.

This axiom states that, in any environment α, any population R_{α} in α contains for some generation m a set D and a pair of sets S' and S which are equivalent with respect to D in both α and β, where β is an environment different from α. Further D is selected for in α and S-D is selected for in β. Thus the axiom guarantees that every population has a chance at some time during its existence to split into two populations which will evolve in different directions. This provides an opportunity for the multiplication of species.

Section 5.3: Different Subpopulations Take Over in Different Environments

With this axiom and some theorems proved in previous chapters, we can prove that the population derived from the subset D of the axiom will take over in environment α, while the population derived from S-D will take over in environment β. The axiom states that there exist two environments, α and β, such that, e.g., short necked giraffes are favoured in α and long necked giraffes are favoured in β; the following theorem states that the descendants of the short necked giraffes will take over in α and the descendants of the long necked giraffes will take over in β.

<u>Theorem 5.1</u>: Let S, D, S', f_α and f_β be the sets and functions of axiom 5.2. Then there exists a generation j such that

$$R'_\alpha(j) = D'^{O}_\alpha(j), \quad R^*_\alpha(j) = D^{*O}_\alpha(j), \quad R'_\beta(j) = \bar{D}'^{O}_\beta(j), \text{ and}$$
$$R^*_\beta(j) = \bar{D}^{*O}_\beta(j).$$

This theorem says that in environment α D will take over regardless of whether S' or $S^* = S-S'$ is in α and that in β $\bar{D} = S-D$ will take over regardless of whether S' or S^* is in β. Actually this does not say that $\bar{D}$ will be eliminated in α or that D will be eliminated in β, for interbreeding may allow them to escape destruction. Remember that a takeover in generation j by D only means that all of the members of the population in generation j are descendants of D; it does not mean that none are descendants of $\bar{D}$ and, in fact, it may be the case that all are descendants of both D and $\bar{D}$. If, on the other hand, it is known that there is no interbreeding between D (and its descendants) and $\bar{D}$ (and its descendants) then it is possible to prove that the one which does not take over will be eliminated. This is stated in the following theorem.

Theorem 5.2: Let S, D, S', f_α and f_β be the sets and functions of axiom 5.2. Let the following pairs of populations be non-interbreeding for all $k \geq 0$:
(1) $D_\alpha^{\prime 0}$ and $\bar{D}_\alpha^{\prime 0}$; (2) D_α^{*0} and $\bar{D}_\alpha^{*0}$; (3) $D_\beta^{\prime 0}$ and $\bar{D}_\beta^{\prime 0}$ (4) D_β^{*0} and $\bar{D}_\beta^{*0}$. Let j be the generation guaranteed by theorem 5.1. Then $\bar{D}_\alpha^{*0}(j) = \emptyset$, $\bar{D}_\alpha^{\prime 0}(j) = \emptyset$, $D_\beta^{*0}(j) = \emptyset$, and $D_\beta^{\prime 0}(j) = \emptyset$.

To illustrate this theorem let us consider the following example. Let S be a set of lions and tigers; let D be the lions and $\bar{D}$ be the tigers. Let S' be a set containing roughly half of the lions and half of the tigers. Let α be an environment where lions are favoured over tigers and β be an environment where tigers are favoured over lions. Now we wish to consider the effects on these organisms if they are in α and compare them with the effects on the organisms if they are in β. Suppose S' is in α and S^* is in β. Then $D_\alpha^{\prime 0}$ is the set of lions in α; $\bar{D}_\alpha^{\prime 0}$ is the set of tigers in α; D_β^{*0} is the set of lions in β; and $\bar{D}_\beta^{*0}$ is the set of tigers in β. Since lions and tigers do not interbreed, the non-interbreeding conditions are fulfilled. Then the theorem states that there is a generation j such that there are no tigers left in α ($\bar{D}_\alpha^{\prime 0}(j) = \emptyset$) and no lions left in β ($D_\beta^{*0}(j) = \emptyset$). The theorem further shows that if the situation had been reversed (i.e. S^* in α and S' in β) the final outcome would have been the same.

Notice that the non-interbreeding conditions of this theorem will hold: (1) if D and $\bar{D}$ are different species; (2) if the set S consists of organisms which reproduce asexually; or (3) if D and $\bar{D}$ just happen not to interbreed during the time required (perhaps because they utilize slightly different parts of the environment though still competing for some resources). Thus the conditions of this theorem are not so restrictive as they might seem.

Section 5.4: Different Environments Generate Different Populations

Now we are in a position to state that, at least under these conditions of non-interbreeding, R'_α cannot be the same population as R'_β (i.e. cannot contain the same organisms); this shows that the two environments will generate different populations from an identical zeroth generation. In fact we will show that after a certain generation j (the takeover generation shown to exist by theorem 5.1), $R'_\alpha(k)$ cannot contain any organism which has a set of ancestors identical with the set of ancestors of any organism in $R'_\beta(k)$. This is not because the probability of the same pattern of mating being repeated twice is very low; $R'_\alpha(k)$ designates any one of the whole set of possible k^{th} generations which can arise in α, so when we say that $R'_\alpha(k)$ contains no organism with ancestor set identical to that of an organism in $R'_\beta(k)$ we mean that in none of the possible k^{th} generations in α and β does such an organism exist. Thus by this generation j the set of possible descendants in α of S' has become completely different from the set of possible descendants in β of S'. This result is stated in the following theorem.

<u>Theorem 5.3</u>: Let S, D, S', f_α and f_β be the sets and functions of axiom 5.2. Let the following pairs of populations be non-interbreeding for all $k \geq 0$:

(1) $D_\alpha^{\prime 0}$ and $\bar{D}_\alpha^{\prime 0}$; (2) D_α^{*0} and $\bar{D}_\alpha^{*0}$; (3) $D_\beta^{\prime 0}$ and $\bar{D}_\beta^{\prime 0}$; (4) D_β^{*0} and $\bar{D}_\beta^{*0}$. Let j be the generation guaranteed by theorem 5.1. Then

(A) $R'_\alpha(k) \cap R'_\beta(k) = \emptyset$ for any $k \geq j$

(B) $R^*_\alpha(k) \cap R^*_\beta(k) = \emptyset$ for any $k \geq j$.

If we consider again the example of lions and tigers used to illustrate theorem 5.2, this theorem states that, even if we suppose that the zeroth generation in α contained exactly the same organisms as the zeroth generation in β, the k^{th} generation (for $k \geq j$) in α contains no organisms that are the same as organisms in the k^{th} generation in β, since only lions remain in α and only tigers remain in β. One possibility that this theorem excludes is that organisms can migrate from α, evolve for a while in a different environment, and then return to α; for, if they could, tigers whose ancestors had found a better home than α might at any time reappear in α, thus contradicting the statement that there exists a generation j such that they disappear forever by j. So we see that α must be simply the sum of the environments of the descendants of $R_\alpha(0)$; α may, to our senses change drastically over the generations and not be the "same" environment at the time of the kth generation as it was at the time of the 0th generation; the only things that may not change are those which are specified by the axioms to be true for all k. In fact, it is even possible for the particular selective pressure favouring H_α^m, as guaranteed by the hereditary variation axiom, to change ~~ever~~ after H^m has taken over, since if $R_\alpha(k) - H_\alpha^m(k) = \emptyset$, $F_\alpha(H_\alpha, R_\alpha, k) > F_\alpha(R_\alpha - H_\alpha, R_\alpha, k) + \Omega$ is always true for $R(k) \neq \emptyset$.

Returning to the position of the tigers which migrate to a better environment, we see that their environment must become a part of α. Thus, if α is a Darwinian Universe, they cannot have migrated to an environment where they are protected from competition by better fitted competitors; the conditions stipulated for α by the theorem are such that if α is Darwinian the tigers will be exterminated in α; any environment in which tigers are not exterminated is either not Darwinian or not as stipulated in the hypothesis of the theorem. They could have migrated to an environment where there were no lions, as long as it was an environment in which they were doomed for some reason. In fact, physical proximity is not a necessary part of "being in the same environment"; the lions and tigers may have always lived on different continents; in this case the relationship between the fitnesses of the lions and the tigers must come from some factor other than direct competition.

Section 5.5: On the Value of Sexual Reproduction

Since the environment of any organisms in R_α is automatically a part of α, we cannot move a population from one environment to another. We can, however, take the set of organisms in one generation of R_α and consider what will happen if they form the zeroth generation of a population R_β. This will be done in Theorem 5.4.

In this theorem we shall investigate the implications of the following type of situation. Let R be a set of bacteria containing two strains T and $R-T$. Let each of these strains contain a subset P which is penicillin resistant and a subset S which is streptomycin resistant. Suppose that the only way for a bacterium to appear with resistance to both drugs is through interbreeding between these two subsets. Suppose further that there is no interbreeding between S and P in strain T, but there is some interbreeding between S and P in strain $R-T$. Then let R be placed in a medium containing penicillin, allowed to remain there until no non-penicillin resistant bacteria remain, and then placed in a medium containing streptomycin. It is clear that no members of strain R-T can survive this treatment, since the lack of interbreeding prevents the formation of doubly resistant bacteria in R-T; on the other hand, some members of strain T can survive, since there are doubly resistant bacteria in T. Thus this situation of an environment in which the selective pressure reverses puts a positive selective value on interbreeding. This is formalized in theorem 5.4, which will be stated following the definition of interbreeding.

<u>Definition 5.2:</u> R'_α and R''_α are interbreeding in k if and only if $R'_\alpha(k) \cap R''_\alpha(k) \neq \emptyset$.

This says that R'_α and R''_α are interbreeding in k if at least one of the k-descendants of $R'_\alpha(0)$ is also a k-descendant of $R''_\alpha(0)$. Thus it includes not only the cases where first generation hybrids (with one parent in $R'_\alpha(k-1)$ and the other in $R''_\alpha(k-1)$) exist in generation k, but also the cases where the actual interbreeding was many generations earlier than k. Note that, in spite of this, it is possible for R'_α and R''_α to be interbreeding in generation k-1 and not interbreeding in generation k; this would happen if no k-1st generation organism with ancestors in both $R'_\alpha(0)$ and $R''_\alpha(0)$ had progeny and there were no first generation hybrids in generation k.

Theorem 5.4: Let S be any set contained in B which satisfies conditions A and B.

Condition A: There exists a set U contained in S which satisfies the following fitness conditions with respect to f_α and f_β :

(1) if $R_\alpha(0) = S$, there exists an $\Omega > 0$ such that $F_\alpha(U^0_\alpha, R_\alpha, k) > F_\alpha(R_\alpha - U^0_\alpha R_\alpha, k) + \Omega$ for any $k \geq 0$

(2) if $j = t(U^0_\alpha, R_\alpha)$, $R_\beta(0) = R_\alpha(j)$, and $(S-U)^0_\beta\ (0) = (S-U)^0_\alpha(j)$ then there exists an $\Omega > 0$ such that $F_\beta((S-U)^0_\beta, R_\beta, k) > F_\beta(R_\beta - (S-U)^0_\beta, R_\beta, k) + \Omega$ for any $k \geq 0$.

Condition B: There exists a set T contained in S such that if $j = t(U^0_\alpha, R_\alpha)$, $T^0_\alpha(0) = T$, $(S-T)^0_\alpha(0) = S-T$, $T^0_\beta(0) = T^0_\alpha(j)$, and $(S-T)^0_\beta(0) = (S-T)^0_\alpha(j)$ then the following interbreeding conditions are satisfied:

(1) T^0_β and $(S-T)^0_\beta$ are non-interbreeding for all $k \geq 0$

(2) $T^0_\alpha \cap U^0_\alpha$ and $T^0_\alpha \cap (S-U)^0_\alpha$ are interbreeding for all $k \geq 0$

(3) $(S-T)^0_\alpha \cap U^0_\alpha$ and $(S-T)^0_\alpha \cap (S-U)^0_\alpha$ are non interbreeding for all $k \geq 0$.

Then if $R_\beta(k) \neq \emptyset$ for any $k \geq 0$, there exists a j' such that $(S-T)^0_\beta(j') = \emptyset$ and $T^0_\beta(j') \neq \emptyset$.

The two fitness conditions in Condition A stipulate that U is a set which is selected for in environment α and whose complement is selected for in environment β. The breeding conditions in Condition B stipulate that the sets T and S-T are such that: 1) the descendants of T do not interbreed with the descendants of S-T in environment β; 2) the descendants of the part of U which is contained in T interbreeds in environment α with the descendants of the part of S-U which is contained in T; and 3) the descendants of the part of U which is contained in S-T do not interbreed in environment α with the descendants of the part of S-U which is contained in S-T. The conclusion then states that under these conditions the set in which interbreeding occurred survives and the set in which interbreeding did not occur does not survive.

This theorem therefore shows that populations which allow interbreeding within the population have survival value in changing environmental conditions over populations which do not. The reason for this is that less fit subpopulations are protected from extermination by interbreeding with the more fit subpopulations; thus interbreeding allows the fitness characteristics of the population which is less fit to be stored, and therefore to be available if the organisms are moved to an environment in which the previously less fit are more fit.

It is interesting to see that this value of sexual reproduction does not depend on the particular mechanics of Mendelian heredity but can be derived from the general laws of natural selection.

With this very interesting result we shall conclude this chapter, which was, after all, only intended to indicate how the Darwinian Universe could be embedded in a universe which contained different environments.

Definition: A Diverse Darwinian Universe is a Biological Universe, a set E of functions f_α, and a set C of populations P_α such that axioms 5.1 and 5.2 are true statements about them.

Notation: $(B, A\!\rhd, =, E, C)$ denotes a Diverse Darwinian Universe.

CHAPTER 5 : APPENDIX

A Diverse Darwinian Universe is a Biological Universe, a set E of functions f_α, and a set C of populations P_α such that the following two axioms hold:

Axiom 5.1: For any f_α in E, $(B, A\!\!>, =, f_\alpha, P_\alpha)$ is a Darwinian Universe.

Notation: Given f_α in E and sets S, $S' \subset S$, and $D \subset S$, the following notation will be used for the indicated subsets:

(1) $S^* = S - S'$

(2) $R_\alpha'(0) = S'$

(3) $R_\alpha^*(0) = S^*$

(4) $D_\alpha'(0) = D \cap S'$

(5) $D_\alpha^*(0) = D \cap S^*$

(6) $\bar{D}_\alpha'(0) = S' - D \cap S'$

(7) $\bar{D}_\alpha^*(0) = S^* - D \cap S^*$

Definition 5.1: A set $S' \subset S \subset B$ is equivalent in generation k to S^* with respect to $D \subset S$ and f_α in E if and only if for any R_α' in P_α and for any R_α^* in P_α, when (a) designates the inequality

$$F_\alpha(D_\alpha'^{\,0}, R_\alpha', k) > F_\alpha(R_\alpha' - D_\alpha'^{\,0}, R_\alpha', k) + \Omega \qquad \text{(a)}$$

and (b) designates the inequality

$$F_\alpha(D_\alpha^{*0}, R_\alpha^*, k) > F_\alpha(R_\alpha^* - D_\alpha^{*0}, R_\alpha^*, k) + \Omega \qquad \text{(b)}$$

Then for any $\Omega > 0$, (a) $\Longleftrightarrow$ (b).

Axiom 5.2: For any f_α in E and any R_α in P, there exists an m such that if $S = R_\alpha(m)$, then there exists $S' \subset S$, $D \subset S$ f_α in E, and $\Omega > 0$ such that

(1) $N(R_\alpha, m) > 0$

(2) R'^{m}_{α} is equivalent in all $k \geq m$ to R^{*m}_{α} with respect to D and f_α.

(3) R'^{m}_{β} is equivalent in all $k \geq m$ to R^{*m}_{β} with respect to D and f_β.

(4) $F_\alpha(D'^{0}_{\alpha}, R'_{\alpha}, k) > F_\alpha(R'_\alpha - D'^{0}_{\alpha}, R'_\alpha, k) + \Omega$ for any $k \geq m$ such that $R'_\alpha(k) \ngeq 0$.

(5) $F_\beta(\bar{D}'^{0}_{\beta}, R'_{\beta}, k) > F_\beta(R'_\beta - D'^{0}_{\beta}, R'_\beta, k) + \Omega$ for any $k \geq m$ such that $R'_\beta(k) \ngeq 0$.

<u>Theorem 5.1</u>: Let S, D, S', f_α and f_β be the sets and functions of axiom 5.2. Then there exists a generation j such that $R'_\alpha(j) = D'^{0}_{\alpha}(j)$, $R^*_\alpha(j) = D^{*0}_{\alpha}(j)$, $R'_\beta(j) = \bar{D}'^{0}_{\beta}(j)$, and $R^*_\beta(j) = D^{*0}_{\beta}(j)$.

Proof: By axiom 5.2 (4) there exists an $\Omega > 0$ such that for any $k > m$, $F_\alpha(D'^{0}_{\alpha}, R'_\alpha, k) > F_\alpha(R'_\alpha - D'^{0}_{\alpha}, R'_\alpha, k) + \Omega$; therefore, by theorem 4.9, there exists a j'_α such that $R'_\alpha(j'_\alpha) = D'^{0}_{\alpha}(j'_\alpha)$. By axiom 5.2 (2) and definition 5.1, axiom 5.2 (4) implies that $F_\alpha(D^{*0}_{\alpha}, R^*_\alpha, k) > F_\alpha(R^*_\alpha - D^{*0}_{\alpha}, R^*_\alpha, k) + \Omega$ for any $k \geq m$; therefore by theorem 4.9 there exists a j^*_α such that $R^*_\alpha(j^*_\alpha) = D^{*0}_{\alpha}(j^*_\alpha)$. Similarly, by axiom 5.2 (5) there exists an $\Omega > 0$ such that for any $k \geq m$ $F_\beta(\bar{D}'^{0}_{\beta}, R'_\beta, k) > F(R'_\beta - \bar{D}'^{0}_{\beta}, R'_\beta, k$ therefore by theorem 4.9 there exists a j_β' such that $R'_\beta(j'_\beta) = \bar{D}'^{0}_{\beta}(j'_\beta)$. By axiom 5.2 (5) and definition 5.1, axiom 5.2 (5) implies that $F_\beta(\bar{D}^{*0}_{\beta}, R^*_\beta, k) > F_\beta(R^*_\beta - \bar{D}^{*0}_{\beta}, R^*_\beta, k) + \Omega$ for any $k \geq m$; therefore by theorem 4.9, there exists a j^*_β such that $R^*_\beta(j^*_\beta) = \bar{D}^{*0}_{\beta}(j^*_\beta)$.

Let j be the largest member of the set $\{j'_\alpha, j'_\beta, j^*_\alpha, j^*_\beta\}$. Then, by theorem 3.4, $R'_\alpha(j) = D'^{0}_\alpha(j)$, $R^*_\alpha(j) = D^{*0}_\alpha(j)$, $R'_\beta(j) = D'^{0}_\beta(j)$, and $R^*_\beta(j) = D^{*0}_\beta(j)$.

Theorem 5.2: Let S, D, S', f_α, and f_β be the sets and functions of axiom 5.2. Let the following pairs of populations be non-interbreeding for all $k \geq 0$:
(1) D'^{0}_α and $\overline{D}'^{0}_\alpha$; (2) D^{*0}_α and $\overline{D}^{*0}_\alpha$; (3) D'^{0}_β and $\overline{D}'^{0}_\beta$; (4) D^{*0}_β and $\overline{D}^{*0}_\beta$. Let j be the generation guaranteed by theorem 5.1. Then $\overline{D}^{*0}_\alpha(j) = \emptyset$, $\overline{D}'^{0}_\alpha(j) = \emptyset$, $D^{*0}_\beta(j) = \emptyset$, and $D'^{0}_\beta(j) = \emptyset$.

Proof: By theorem 5.1 there exists a j such that $R'_\alpha(j) = D'^{0}_\alpha(j)$, $R^*_\alpha(j) = D^{*0}_\alpha(j)$, $R'_\beta(j) = \overline{D}'^{0}_\beta(j)$, $R^*_\beta(j) = \overline{D}^{*0}_\beta(j)$. Since D'^{0}_α and $\overline{D}'^{0}_\alpha$ are non-interbreeding for all $k \geq 0$, $\overline{D}'^{0}_\alpha(j) \subset R'_\alpha(j) - D'^{0}_\alpha(j)$; but $R'_\alpha(j) = D'^{0}_\alpha(j)$ implies that $R'_\alpha(j) - D'^{0}_\alpha(j) = \emptyset$; therefore $\overline{D}'^{0}_\alpha(j) = \emptyset$.

The remaining three equations in the conclusion of the theorem follow by exactly analogous arguments.

Theorem 5.3: Let S, D, S', f_α and f_β be the sets and functions of axiom 5.2. Let the following pairs of populations be non-interbreeding for all $k \geq 0$:
(1) D'^{0}_α and $\overline{D}'^{0}_\alpha$; (2) D^{*0}_α and $\overline{D}^{*0}_\alpha$; (3) D'^{0}_β and $\overline{D}'^{0}_\beta$; (4) D^{*0}_β and $\overline{D}^{*0}_\beta$. Let j be the generation guaranteed by theorem 5.1. Then

(A) $R'_\alpha(k) \cap R'_\beta(k) = \emptyset$ for any $k \geq j$

(B) $R^*_\alpha(k) \cap R^*_\beta(k) = \emptyset$ for any $k \geq j$.

Proof: (A) Suppose k' is an integer greater than or equal to j, and suppose there exists an organism O such that O is in $R'_\alpha(k') \cap R'_\beta(k')$. Then O is in $R'_\beta(k')$, which implies, by theorems 5.1 and 3.4, that O is in $\overline{D}'_\beta(k')$; therefore there exists an O' in $\overline{D}'^{O}(O)$ such that $O \lhd O'$. On the other hand O in $R'_\alpha(k') \cap R'_\beta(k')$ implies that O is in $R'_\alpha(k')$. Now since there exists O' in $\overline{D}'^{O}_\beta(O) = S-D$ such that $O \lhd O'$ and since O is in $R'_\alpha(k')$, O must be in $\overline{D}'^{O}_\alpha(k')$. But by theorem 5.2, $\overline{D}'^{O}_\alpha(k') = \emptyset$. Since O cannot be in the null set, this is a contradiction. Therefore there exists no such O, so $R'_\alpha(k') \cap R'_\beta(k') = \emptyset$.

(B): The proof of (B) is exactly analogous.

<u>Definition 5.2</u>: R'_α and R''_α are interbreeding in k if and only if $R'_\alpha(k) \cap R''_\alpha(k) \neq 0$.

<u>Theorem 5.4</u>: Let S be any set contained in B which satisfies conditions A and B.

Condition A: There exists a set U contained in S which satisfies the following fitness conditions with respect to f_α and f_β:

(1) if $R_\alpha(O) = S$, there exists an $\Omega > 0$ such that $F_\alpha(U^O_\alpha, R_\alpha, k) > F_\alpha(R_\alpha - U^O_\alpha, R_\alpha, k) + \Omega$ for any $k \geq 0$.

(2) if $j = t(U^O_\alpha, R_\alpha)$, $R_\beta(O) = R_\alpha(j)$, and $(S-U)^O_\beta(O) = (S-U)^O_\alpha(j)$, then there exists an $\Omega > 0$ such that $F_\beta((S-U)^O_\beta, R_\beta, k) > F_\beta(R_\beta - (S-U)^O_\beta, R_\beta, k) + \Omega$ for any $k > 0$.

Condition B: There exists a set T contained in S such that if $j = t(U_\alpha^0, R_\alpha)$, $T_\alpha^0(0) = T$, $(S-T)_\alpha^0(0) = S-T$ $T_\beta^0(0) = T_\alpha^0(j)$, and $(S-T)_\beta^0(0) = (S-T)_\alpha^0(j)$ then the following interbreeding conditions are satisfied:

(1) T_β^0 and $(S-T)_\beta^0$ are non-interbreeding for all $k \geq 0$

(2) $T_\alpha^0 \cap U_\alpha^0$ and $T_\alpha^0 \cap (S-U)_\alpha^0$ are interbreeding for all $k \geq 0$

(3) $(S-T)_\alpha^0 \cap U_\alpha^0$ and $(S-T)_\alpha^0 \cap (S-U)_\alpha^0$ are non-interbreeding for all $k \geq 0$.

Then if $R_\beta(k) \neq \emptyset$ for any $k \geq 0$, there exists a j' such that $(S-T)_\beta^0(j') = \emptyset$ and $T_\beta^0(j') \neq \emptyset$.

Proof: By Condition A,(1), and theorem 4.9, $j = t(U_\alpha^0, R_\alpha) < \infty$. Since any sublineage of a population satisfies axioms 4.1, 4.2 and 4.3 theorem 4.9 can be used with sublineages. Therefore by Condition B,(3), the conditions of theorem 4.10 are satisfied for sublineages $(S-T)_\alpha^0(k) \cap (S-U)_\alpha^0(k)$ and $(S-T)_\alpha^0(k) \cap U_\alpha^0(k)$; by theorem 4.10 $(S-T)_\alpha^0(j) \cap (S-U)_\alpha^0(j) = \emptyset$. Therefore $(S-T)_\beta^0(j) \cap (S-U)_\beta^0(j) = \emptyset$ and so $(S-U)_\beta^0(0) \subset T_\beta^0(0)$; by theorem 3.5, $(S-U)_\beta^0(k) \subset T_\beta^0(k)$ for any $k \geq 0$. So, by Condition B,(1) $(S-T)_\beta^0(k) \cap (S-U)_\beta^0(k) = \emptyset$, for any $k \geq 0$. Therefore

$$(S-T)_\beta^0(k) \subset R_\beta(k) - (S-U)_\beta^0(k) \quad \text{for any } k \geq 0. \qquad (a)$$

Now, by Condition B,(2), $(S-U)_{\alpha}^{0}(j) \neq \emptyset$; therefore $(S-U)_{\beta}^{0}(0) \neq \emptyset$. So by Condition A,(2), and Theorem 4.9, there exists $j' = t((S-U)_{\beta}^{0}, R_{\beta})$ such that $R_{\beta}(j') - (S-U)_{\beta}^{0}(j') = \emptyset$. Therefore, combining this with (a) above

$$(S-T)_{\beta}^{0}(j') = \emptyset \qquad \text{(b)}$$

Since $R_{\beta}(k) \neq \emptyset$ for any $k \geq 0$, (b) implies that

$$T_{\beta}^{0}(j') \neq \emptyset.$$

CHAPTER 6 : CONCLUSION

In the previous three chapters the axioms necessary to a theory of natural selection have been explicitly stated, along with some of the theorems which can be derived from them. The discussions in these chapters have been, necessarily, concerned with the details of the system in order to justify and clarify the statements. The discussions in this chapter will be concerned with characteristics of the axiom system as a whole in order to indicate the type of clarification which the axiomatization provides.

Section 6.1: The Structure of the Theory

To what extent does the structure of the axiom system reflect the underlying structure of evolutionary theory? (Note that we here use the term "evolutionary theory" instead of "the theory of natural selection" because the Diverse Darwinian Universe includes more than the theory of natural selection.) The Diverse Darwinian Universe presupposes the Darwinian Universe, which presupposes the Biological Universe; does this structure of three nested sets of axioms reflect an intrinsic property of evolutionary theory or is it merely an arbitrary device of presentation?

That this does indeed reflect an intrinsic property of evolutionary theory is indicated by the fact that the stages in the historical development of the theory closely correspond to the stages in the axiomatic development: the Biological Universe describes pre-Darwinian theory; The Darwinian Universe describes Darwinian theory; and the Diverse Darwinian Universe describes post-Darwinian theory. It is further indicated by the fact that each axiom set introduces a new undefined concept and uses this concept to place additional structure on the previously defined universe; clearly the additional structure made possible by these new undefined concepts corresponds to new ideas which are not contained within the previously defined universe and thus, since these ideas are the elementary ideas of the theory, the axiom sets must reflect the underlying structure of the theory. The axiomatic method, therefore, provides a means for discovering the underlying logical structure of the theory.

Section 6.2: Interpretations of Fitness

The axiomatic method provides, also, a controlled flexibility which will allow us to explore the possibility of natural selection in universes different from the one in which we live and thus to discover both the generality of the concept and the factors in our universe which particularize it. In this section we will consider universes in which the interpretation of the undefined term "fitness" differ, but the method that will be used could be applied equally well to clarify any of the other undefined terms.

Although the term "fitness" has never been defined, both the reader and I have some interpretation of what it means in natural selection. (My conception is of a combination of reproductive potential with a potential for obtaining food and avoiding dangers.) Similarly we have interpretations of the meanings of the other undefined terms. Without such interpretations of the undefined terms an axiom system has no meaning; it is just a meaningless set of relationships in which no one is particularly interested. A set of such interpretations which assigns a meaning to each of the undefined terms of an axiom system such that the axioms are true statements is called an interpretation of the axiom system. Now, in fact, I believe that the set of interpretations which has been implied in the descriptive part of this thesis forms an interpretation of the axiom system; however it is clearly impossible to prove that the axioms are true statements about them (this would be equivalent to proving that evolutionary theory truly describes the real world), so this can only be called a possible interpretation. It is interesting to realize that there are other possible interpretations of the axiom system, which would correspond to a realization of the axiom system within a universe different from our own.

Let us consider a different interpretation of fitness. Suppose the universe were such that food was available without limit and all organisms in any generation had exactly the same life span, this life span being limited by the condition that the number alive at any one time was fixed; thus suppose that differential reproductive ability was the sole difference according to which individuals could be selectively superior or inferior. If we then conceive of f as being a measure of reproductive ability, then the set consisting of this interpretation of the meaning of f plus our usual interpretations of the meanings of the other undefined terms is a possible interpretation of the axiom system; that is, the axioms will be plausible statements about the relationships between f, organisms, ancestors, etc. We could use this possible interpretation to deduce the results that would be expected in such a population which was selected only on reproductive ability; the results that could be thus deduced would, of course, be exactly the same as the results deduced when considering any other interpretation of the meaning of fitness, but the interpretation of the results would be different; that is, the structuve of the results would be the same though their meanings would be different.

We could consider, on the other hand, a universe such that the organisms differed (hereditarily) only in their ability to obtain food. Then we would conceive of f as being simply a measure of the ability to obtain food; this interpretation of the meaning of f plus our usual interpretations of the meanings of the other undefined terms provides another possible interpretation of the axiom system. The survival of the fittest axiom would, of course, only be plausible if in this universe superiority in the ability to obtain food led to superiority in the number of descendants.

Clearly the list of possible interpretations could be extended indefinitely, with f defined in each case as the only factor (or set of factors) in which the organisms differed hereditarily and such that superiority in the factor will lead to superiority in the number of descendants. In other words, if all other possible components of fitness are held constant, whatever is left will give a plausible interpretation of the axiom system. Therefore, no matter what component of "total fitness" we choose to think of as fitness we would derive the same axiom system to describe natural selection as long as we considered all other components to be negligible. This is the reason that Darwin, with a rather different conception of fitness from that of the statistical geneticist, was able to derive a theory which is, in all of its essential points, accepted by the statistical geneticist. The different meanings that Darwin and the statistical geneticist (or you and I) have for the most important concept in the theory do not lead to a necessity to develop different theories, because it is the theory rather than the intuitive meaning which determines the meaning of fitness.

Section 6.3: Possible Systems of Heredity

We have, in the previous section, discussed the flexibility of the axiomatic method in terms of the differing possible interpretations of the undefined terms; in this section we shall discuss its flexibility in terms of the different sets of axioms that may be added to a given axiom system. It will be an informal discussion, for the different systems of heredity which will be discussed have not themselves been axiomatized and therefore cannot be formally proved to be independent of and consistent with the Diverse Darwinian Universe.

We shall consider three systems of heredity and their possible relationship with the Diverse Darwinian Universe. First consider the blending theory of heredity, which postulates that the hereditary characteristics of an organism are a combination of the average of the hereditary characteristics of its parents and some new, non-parental, characteristics; if the non-parental characters are related to fitness and if there are enough but not too many of them, then this system of heredity will be consistent with the Diverse Darwinian Universe and axioms defining this system could be combined with the axioms of the Diverse Darwinian Universe to give predictions about the progress of evolution within such a system. Next consider the Lamarckian theory of heredity, which postulates that the hereditary characteristics of an organism are a combination of some of the hereditary characteristics of its parents together with some characteristics acquired during its lifetime; if the acquired characteristics are related to fitness and if there are enough but not too many of them, then this system of heredity will be consistent with the Diverse Darwinian Universe and axioms defining this system could be combined with the axioms of the Diverse Darwinian Universe to give predictions about the progress of evolution within this system. Lastly, consider the Mendelian theory of heredity, which postulates that the hereditary characteristics of an organism are a combination of a particular type of set of some of the hereditary characteristics of its parents and some new, non-parental, characteristics; if the non-parental characteristics are related to fitness and if there are enough but not too many of them, then this system of heredity will be consistent with the Diverse Darwinian Universe and axioms defining this system could be combined with the axioms of the Diverse Darwinian Universe to give predictions about the progress of evolution within this system. From these examples it is clear that Mendelian heredity occupies no special logical position with respect to the theory of natural selection; it may be replaced by another, contradictory, system of heredity without any change being made in the theory of natural selection.

The combination of Mendelian heredity and the theory of natural selection would, however, be of special interest to us, for it would be particularly useful to be able to derive the consequences of a system in which survival is determined by natural selection and heredity is determined by the Mendelian laws. Such a system could be formed by simply adding to the axioms defining the Darwinian Universe a set of axioms corresponding to the Mendelian laws. It would be of interest to see how the conclusions of such a system would compare with the conclusions of the statistical geneticist, for the statistical geneticist uses, as crude approximations, so many assumptions that are known to be false (e.g. random mating, constant selective value, etc.) that his conclusions, although valuable in indicating the potentialities of natural selection in a universe with Mendelian heredity, are not reliable in detail. On the other hand, the system suggested, while completely unable to discuss events over a short time period, should be completely reliable in the statements it does make. Therefore each system might provide information in the area of the blind spot of the other system.

Section 6.4: Extent of Achievement of Purpose

What are the basic assumptions of the theory of natural selection? The author would assert that this thesis completely answers this question. The assumptions are stated in the axioms of the Darwinian Universe; the theorems proved with the axioms are evidence that these are, in fact, the assumptions of natural selection, for the theorems are all intuitively derivable consequences of the intuitive concept of natural selection. It is impossible to state the contribution of the thesis in terms of its answering more specific questions which have been raised in the literature, for the contribution is, rather, in reducing the amorphous confusion prevalent in the statement of the theory.

However one specific contribution can be clearly seen in the clarification of the tautological nature of the concept of fitness in the theory of natural selection. This clarification may prove to be of value not only to those interested in natural selection but also to those interested in taxonomy, for the tautological nature of the traditional theory of biological classification is of serious concern to taxonomists and is one of the major weapons used by numerical taxonomists to discredit classical taxonomy;(23,24) probably an axiomatization of the theory of taxonomy would provide taxonomists with an understanding of the reason that classical taxonomy, like natural selection, has been so fruitful in spite of its obviously tautological nature. Thus the axiomatization in this thesis provides the answer to at least one question which has worried biologists and provides a method of answering another.

What are the implications of the assumptions of the theory of natural selection? It is clear that I have only begun the exploration of the consequences of this axiom system. No attempt has been made to derive new and astounding results, for such results will be of interest only after the system has been shown to generate the expected intuitive results. Thus the theorems have been aimed at showing that the axioms have reasonable, expected consequences (e.g. the oscillation around a stability point when the selective advantage is density dependent, and the differences between natural selection in interbreeding populations and natural selection in non-interbreeding populations) and that certain consequences that must be derivable in any theory of natural selection (e.g., the phenomenon of subpopulations taking over) can be derived; this aim has been reasonably well achieved. However the important result of the thesis is not the set of theorems but the axiom system itself, which, though incomplete for the description of evolutionary theory, does give a precise logical statement of the Darwinian theory of natural selection.

REFERENCES

(1) Charles Darwin; The Origin of Species; 6th ed. Everyman's Library, J.M. Dent and Sons, Ltd., London, 1928 (first published 1859); p.124.

(2) Julian Huxley, A.C. Hardy and E.B. Ford, eds; Evolution as a Process; George Allen and Unwin Ltd., London, 1958, pp.1,2.

(3) Ernst Mayr; Animal Species and Evolution; The Belknap Press of Harvard University Press, Cambridge, Mass. 1963, p.1.

(4) Mayr, p.30.

(5) Th. Dobzhansky; Speciation as a Stage in Evolutionary Divergence; The American Naturalist, (1940), LXXIV; pp.312-321.

(6) Mayr; pp.12-30.

(7) Ronald A. Fisher; The Genetical Theory of Natural Selection; 2nd ed. Dover Publications, Inc. New York, 1958 (first published 1929;) pp.22-51.

(8) W.D. Hamilton; The Genetical Evolution of Social Behaviour, I; J. Theoret. Biol. (1964), VII; pp.1-16.

(9) J.H. Woodger; The Axiomatic Method in Biology; Cambridge University Press, Cambridge, 1937.

(10) N. Whitehead and B. Russell; Principia Mathematica, To *56, Cambridge University Press, 1964.

(11) J.H. Woodger; *Biology and Language*; Cambridge University Press, Cambridge, 1952; pp.219-252.

(12) John R. Gregg; *The Language of Taxonomy*; Columbia University Press, New York, 1954.

(13) J.H. Woodger; Theorems on Random Evolution; Bull.Math. Biophysics, *XXVII* (1965); pp.145-150.

(14) N.A. Barricelli; Numerical Testing of Evolution Theories; Parts 1 and 2; Acta Biotheoretica, *XVI*, (1962) pp.69-98 and 100-126.

(15) Mayr, p.12.

(16) Darwin; *loc.cit.*

(17) Fisher; *op.cit.*

(18) William Feller; On the Influence of Natural Selection on Population Size; Proc.N.A.S., *LV*, (1966) pp.733-737.

(19) W.D. Hamilton; The Moulding of Senescence by Natural Selection; J.Theoret. Biol. *XII*, (1966); pp.12-45.

(20) Mayr; p.183.

(21) Darwin; *loc.cit.*

(22) Darwin; *loc.cit.*

(23) Robert Sokal and Peter Sneath; *Principles of Numerical Taxonomy*; W.H. Freeman and Company, London, 1963.

(24) David L. Hull; Certainty and Circularity in Evolutionary Taxonomy; Evolution, *XXI*, (1967), pp.174-184.