

1. Introduction

This thesis will argue that there exists a unit of cultural knowledge that is analogous to the gene of biological evolution. This unit has been referred to as a “meme” by Richard Dawkins (1976). Both genes and memes vary and these variations survive differentially. The consequence of this differential survival is evolution. Further, this thesis will argue that there is only a *single* process underlying both gene and meme multiplication. Yet, because the units of knowledge, genes and memes, operate in distinctly different environments (the physical environment surrounding an organism and the mental environment of a meme), there appear to some people to be two distinct processes operating.

Central to this single process is the work of Charles Darwin (1859). Darwin borrowed from the economic theories of Malthus:

Population, when unchecked, increases in a geometric ratio. Subsistence increases only in an arithmetical ratio. A slight acquaintance with numbers will shew the immensity of the first power in comparison of the second. By that law of our nature which makes food necessary to the life of man, the effects of these two unequal powers must be kept equal. This implies a strong and constantly operating check on population from the difficulty of subsistence. This difficulty must fall somewhere; and must necessarily be severely felt by a large proportion of mankind (Malthus 1798:14).

Malthus realised that there is a struggle for existence, a point not lost on Darwin who argued similarly:

As many more individuals of each species are born than can possibly survive; and as, consequently there is a frequently recurring struggle for existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be naturally selected (1859:68).

Evolution is the result of the differential survival of these variations.

Darwin was not alone in his ideas on evolution and in his preface to the *Origin of the Species*, he lists some 34 others who had similarly concluded that life evolved and was not created. One of these was Lamarck who also postulated that species evolved through inherited changes. However, Lamarck's suggestion that evolution occurs by the passing of acquired characters we now know to be incorrect. At the time, as the mechanism of genetic inheritance was unknown, it seemed a reasonable belief. Lamarck's example of the giraffe obtaining a longer neck through continual stretching, and the passing of "stretched neck" characteristics to its offspring, is well known (Huxley 1964). In one sense his suggestion is not totally incorrect. A mutation within a germ cell is a change acquired during the lifetime of an organism, yet the change is a random one (or at least there is a random component), not a change generated through any behaviours of the organism. After reproduction there is a variation in the offspring through this mutation and it is the consequent differential survival of these offspring that we now take as the central idea in evolution. The discovery of genes and their method of transmission has given evolution theory a solid foundation. This expanded view is often referred to as "neo Darwinism" or the "modern synthesis".

Four chapters follow this Introduction. In the second chapter, immediately following, I attempt to explain how particular words are used within the thesis. These distinctions are crucial for later arguments and include ideas on what constitutes an "environment", the meaning of "randomness", "chaos" and "exactness". This clarification is necessary as many authors have used phrases such as "a random mutation" or "the organism was unfit in its environment" while failing to explain exactly what is meant by the terms they contain.

In the third chapter I will consider genes as knowledge in the sense that, through the differential survival of organisms in past environments, genes represent knowledge of those environments. Donald Campbell (1974) and Konrad Lorenz (1977) saw the innate knowledge of animals as genetic knowledge; knowledge that has been gained through the interaction of ancestral organisms with their environments. The mechanism of the formation of this "phylogenetic knowledge" requires a study of concepts such as fitness, selection and adaptation. Throughout, I will stress the coevolutionary nature of the environment/organism relationship, wherein the organism changes its environment while at the same time the environment changes the organism.

The fourth chapter continues the study of knowledge, however, instead of genetic knowledge I will consider cultural knowledge. This is knowledge passed from person to person, not through the genes, but as ideas stored within minds. I will adopt the term "meme" for this unit of knowledge (Dawkins 1976). Genes and memes and their similarities and differences are considered. Such an approach was taken by Karl Popper (1959) and Thomas Kuhn (1970). They compared the change of scientific ideas with the change in biological species. There are many similarities; both show periods of stasis until a variation occurs (in the form of a gene mutation or a new scientific idea); and the variations, if successful, replace the previous gene or scientific idea. Each multiplies in its own

environment. I will argue that there is a single process underlying meme and gene multiplication. The meme is selected for its ability to survive in a sea of minds, the meme pool; a mental equivalent of the primordial soup of replicating chemicals from which life arose. The meme replicates in another mind by that mind's imitation of it. This is somewhat controversial yet an increasing number of people are taking Dawkins' suggestion (memes are replicating entities in their own right) seriously.

Various objections to the notion of the "meme" have been made but I believe these can be overcome. At least some rejection of the idea of "memes" is due to it being a radically new belief that will change our whole perception of life. People resist change. Any new belief system faces an initial rejection as people are comfortable with established beliefs. The greater the difference between the new system and the previous system, the greater the resistance to adopting it. A new idea in physics, if it can be confirmed by further experiments, is readily adopted. Evolution theory, with its inherent random component and gradual nature, does not lend itself easily to study. The evolution of ideas is considerably faster than genetic change and in this respect, a study should be easier. On the other hand, there is a greater difficulty locating the meme as a physical unit in the brain, as compared with the gene within the organism. Hopefully this will become clearer as our understanding of the mind increases. But for the present, the idea of "memes" is relatively new and so, to achieve anything, the nature of this thesis must be, to some extent, speculative.

Dawkins, with his idea of "memes", is suggesting no new physical concepts or presenting any new data. Rather he is taking a different view of what is essentially the same story that we already know. That is, knowledge changes through learning. To illustrate this he uses the example of a Necker Cube (1982). One form is seen first and, after a period of concentration, it changes to that of another form. Similarly, a

picture may have two figures within it, the mind seeing one first, and then later swapping to a second image. The use of the "meme" is a new way of seeing the transfer of ideas between people.

In contrast, others have appealed to new physical fields or forces for the transfer of ideas. For example, Sheldrake (1982) suggested that information exchanges between organisms can occur via "fields" which he termed morphogenetic fields. A new idea that an animal has enters a medium where it can influence new minds by increasing the likelihood of the formation of that idea in that new mind. The new idea "encourages" its replication as new minds tap into the morphogenetic field. He has given many examples yet none seem to be widely accepted as genuine. For example, potato washing monkeys, who took six years to develop this habit, somehow transferred this knowledge (it is argued) to monkeys on a neighbouring island which achieved this feat in considerably less time. However it is more likely that this example is a case of the incorrect reporting of the true events (Woodhouse 1992:37). As well as experimental problems, logical problems also arise with Sheldrake's ideas. If knowledge is transferred with its influence depending on its frequency, then a new idea should be outweighed by the cumulative affect of all the previous ideas it is trying to replace. A new idea would not be able to get started as a person taking up the new idea would have to choose it over the stronger influence of the older idea which dominates the morphogenetic field (Smith 1992:57-58).

I have used the example of Sheldrake to emphasise what I am not trying to do; that is, to posit new physical concepts such as morphogenetic fields. Lamarckian inheritance also fails for this reason. It suggests a physical path through which acquired information could progress. For transmission of an acquired character, the action of the giraffe's excessive stretching of its neck would need to be transferred to the next generation. For this to occur, in the germ cell there would need to be encoded

information that says "increase neck length". There is no evidence of a physical mechanism that achieves this. In contrast, the idea of the "meme" does not require any new physical mediums for transferral. That cultural information is passed through the senses is well established. Rather, the focus of this thesis is to consider whether the meme is an autonomous living entity in its own right. If so, the idea of the meme represents a move away from a human centred view of knowledge. While a new meme is a product of an individual, once it has spread through the "meme pool" it is more a property of the society than its originator.

Any biological or philosophical description is to some extent metaphorical. Both images of the Necker Cube are metaphors of the cube's total image. People may use a metaphor for understanding a particular idea yet at the same time realise that it is a metaphor and once the understanding is gained the metaphor can be discarded. The student of physics' first description of electrical resistance and current flow may be explained through an analogy to the movement of water in pipes. Voltage is the water pressure, resistance is the pipe diameter and the rate of flow that results is the amperage. However once the electrical circuit is understood, the metaphor can be discarded. It is a convenient model for transition but not a goal in itself.

Similarly, the discussion below is to some degree metaphorical and much of the metaphorical framework can be discarded once understood. No worded phrase is as good as the meaning behind it. For example, the very word "gene" has been used in many different ways and still defies exact definition yet it will be used countless times below. Once inheritance is understood, the word "gene" is no longer needed. The idea of inheritance is not dependent on genes, and, if there are other organisms on other planets, the "gene" could just as well apply to these organisms' units of information. Evolution is a universal principle not

confined to this planet nor to the gene. The idea of the meme is also metaphorical in the sense that it is an approximation of an exact process of information transferral. Yet this thesis will claim that the use of the “meme” as an autonomous living entity is a better metaphor than our current understanding of cultural inheritance. Both Newton and Einstein’s equations describe the motion of an object, yet the latter are more exact and so is a better metaphor of reality than the first. Like Einstein’s equations, the concept of the meme represents a more exact understanding of life as it is than our current understanding.

Lastly, the fifth chapter attempts to use the concept of the “meme” and apply it to some of the understandings and activities of humankind. The ideas developed in previous chapters will be used as logical tools from which a new interpretation of such topics as myth, medicine, environmental economics, materialism and population control, can be made. These topics represent only a selection of many possible topics and are by no means intended to be exhaustive. The purpose of this chapter is to gauge the usefulness of the meme and determine whether such a concept helps in comprehending our real world.

In chapters 4 and 5 I will choose those examples (where a number of alternative examples are possible) that most highlight today’s social injustices. This may give a political element to the thesis that is not usually seen in biological or philosophical studies. Such an approach not only should be followed but must be followed. Not to do so is to ignore one’s responsibility to humankind. For example, a biological study of an endangered species is incomplete unless it addresses the issue of *why* the species is endangered.

The English language has traditionally used he/him to represent both male and female in the third person. For convenience in this thesis, a

sentence that starts with "A person" may later use the pronoun "he" or "him". I hope the reader will take this as "he/she" and "him/her".

The following chapters are divided into sections. At the end of each of section I have tried to indicate, in a few lines marked by *italics*, not a summary of the arguments made, but the main point(s) reached by those arguments.

2. Terms

Any investigation of knowledge must first establish the meaning of key terms that will form the basis of the investigation. This section will restrict itself to such terms as are essential to the framing of following chapters.

2.1 The Environment

Everything external to an organism can be considered its environment. An organism interacts with its environment, taking from it energy and materials for growth, respiration and reproduction. Plants use sunlight, water and carbon dioxide to construct the carbon chains that form the basis of organic matter. Animals consume plants as well as other animals and use this stored energy for their own construction. An organism is selectively advantaged by its ability to make "sense" of its environment. That is, an organism must be able to function in its environment such that it can survive and reproduce. Those organisms not making sense of it do not fare well and, on average, leave fewer offspring.

Lifeforms in an organism's environment are active; plants are growing, animals are moving about and animals with developed brains are thinking. Physical processes, such as night and day and gravity, are all ongoing. Due to this activity an organism's environment is in flux; continuously changing. As such it would be more correct to say that an organism is surrounded by a series of environments, each of an infinitely small time period. An organism's environments may vary significantly. An eagle's environment may range from forest in the summer to desert in the winter, with a great number of different foods utilised and temperatures experienced. A worm may, on the other hand, not range more than a few metres from its origin and, given the uniformity of some

soils, experience almost no environmental variation. For convenience, rather than continually refer to an organism as surrounded by series of environments, I will retain the word "environment" for this larger meaning, yet use "environments" where possible.

The complexity of every organism makes it unique. Even the characteristics of just a single cell, the exact number of chemicals and their spatial orientation, could not simultaneously occur in another cell. This difference between cells is not necessarily great for, say, a colony of yeast cells. Here multiplication is asexual and cells are genetically identical, though not identical in water content, proteins and so on. The more complex the organisms, the greater the differences likely between them. As an organism is unique, the environment it experiences must also be unique.

The environment of an organism is theoretically infinite and contains all other organisms. Yet the major influences on an organism are usually quite localised. Only a small fraction of the organisms in a particular environment will directly interact with that organism and these are generally located within its immediate vicinity. For example, an amoeba interacts directly with another organism through contact. If an amoeba consumes a particle of food then this represents one less particle that may have afforded a meal to another amoeba. By interacting with its environment, the amoeba has changed that environment. A worm that digests amoebas ingested with soil particles, increases the fertility of that soil (through releasing the nutrients within the amoeba) and so improves plant growth. A bird eats the worm and so on. But connections between organisms need not be so direct. Fish live in a watery environment yet may be hunted by land animals. Earthworms live in the soil yet their food comes from vegetable matter that was once above the ground. An organism's connection to different parts of its environment depends on

its activities and habits. Each organism is part of the overall biomass, and so each affects, directly or indirectly, all other organisms.

For a worm, a rabbit is no threat yet a bird is a considerable danger. If each is the same distance from the worm, the bird is much more likely to affect the worm's well-being. Thus the components (in this case, a rabbit or bird) within an organism's environment differentially affect that organism. An organism differentially interacts with its environment. The distance of a predator is not the only factor, as there is also the mental state of other animals. A worm may or may not be eaten depending on the *intention* of the bird, that is, whether it is hungry. Organisms, such as humans, have complex interactions with their environments, with the mental state of other humans being a significant part of that environment. A letter from a distant friend may have more impact on a person's behaviour than the action of someone living in close proximity.

The part of an organism's environment that it interacts with consistently, that is, those components most frequently associated with its life, is generally called the organism's niche. A niche is a subset of the total environment of an organism. A bird will be part of a worm's niche while a rabbit will not (at least not so directly).

An environment differentially effect an organism. The worm, by feeding on soil and so the micro-organisms in it, assists with the breakdown of organic material. Through the tunnels made, the soil is aerated. The worm eaten by the bird has also altered its environment (and died in the process) by fulfilling the hunger of the bird. An organism differentially affects its environment. A single worm will make little change. To go to the other extreme, a person like Stalin directly caused the deaths of millions of people. Had there been a slight variation in the environment of Stalin's parents (being born in a different street, having different friends, not having met at all and so on) then this variation could have

led to a different child being born. Even given the birth of Stalin, different circumstances in his upbringing may have produced a different person. Many coincidences were needed to produce the outcome that occurred. The extent of change caused to the environment varies from organism to organism.

An organism's environment is everything external to it. Both organism and environment are unique. Components of an environment with which an organism has particular interaction, make up an organism's niche.

2.2 Randomness and Chaos

If evolution is the differential survival of variations, with those variations being "random" mutations, then a study of the meaning of "randomness" in an evolutionary context is essential.

Random generally means "happening by chance". For example, in throwing a coin, either a head or a tail occurs randomly. However this randomness is from the reference frame of the thrower of the coin. The result of the throw cannot be predicted by the person throwing the coin, so to him the throw is random. However others have argued that "... the upward velocity of the coin, the rate of spin, and Newton's laws all determine where the coin will land" (Kolata 1986:1069). A person with the ability to make the appropriate calculations from knowing the initial conditions before the throw, can calculate the outcome of the throw. If this is the case the outcome is not random to the calculating person. Consider a simpler case. Imagine that the throw of the coin is modified such that the person now pulls a lever which projects the coin into the air. Say the lever is connected to a computer that is able to calculate the outcome of the throw by measuring the force applied to the lever. To the person pulling the lever, who cannot make these calculations, the outcome of the throw is still, to him, random, yet it is not random to

those people reading the calculation done by the computer. The result, if the speed of calculation is quick, can be known to them before the fall of the coin. It is not random in the reference frame of those reading the calculations.

Consider the drawing of a lottery. Say a lottery is drawn in advance of the sale of the tickets. The drawer then knows which is the winning ticket. Should the drawer then observe the number of a lottery ticket being purchased by another person, he will know whether the ticket is the winning ticket or not. This is no help to the purchaser though. From his reference frame his chance of winning still has a certain probability depending on the total number of tickets sold. From the reference frame of the purchaser of the ticket, his chance of winning is clearly random, while to the drawer it is not random.

In the above examples I have used a human as the reference frame from which events have been observed. Now it must be asked whether there is a reference frame from which *any* event can be predicted or “known”, not necessarily a human centred reference frame. There are problems with such a suggestion. The first would be, what is the nature of the entity that is at the centre of this reference frame? In the case of the computer that calculates the fall of the coin, this machine would represent a reference frame from which the coin’s outcome is predictable. Here the computer “knows” the outcome of the toss, whether or not someone is reading its output. While an event may seem random from a particular human reference frame, should there exist another reference frame from which the event is “known”, then this event is still not random, in a general sense. That is, if there exists *any* reference frame from which an event is not random, then the event is determined.

Consider a particular molecule within a gas. Does this molecule “know” about the behaviour of the other molecules. Certainly it experiences their

gravitational forces and electric and magnetic fields. The mathematician, Laplace, saw the resulting behaviour as mechanical determinism (Flew 1979). He argued that the velocities and masses of two molecules before their collision determined the resulting velocities after that collision. If this is the case, a molecule "knows" its future path through its experience of the forces and fields before collision. While the behaviour of the gas molecule seems random to us, it may not be random to the molecule itself, that is, random from its reference frame. If this is the case it would suggest a determined world. This question is the essence of whether there is real randomness or not. For an event to be indeterminate, it must be indeterminate from *all* reference frames. Should there be a reference frame from which the outcome of the event is known, then the event is determined.

Like randomness, the meaning of chaos varies, depending on the reference frame used. From our reference frame an event may appear chaotic but this does not imply that there are no other reference frames from which the event is known. Some scientists believe that chaos exists as an inherent property of the atomic structure. Gribben (1990), in an article about the physicist, John Bell, entitled "The Man who Proved Einstein Wrong", uses Bell's Theorem to demonstrate the inherent indeterminism in the behaviour of fundamental particles such as electrons. However this theorem has been disputed by Shanks, who states: "Bell's argument is certainly valid. But should one grant all the assumptions upon which it rests?" (1991:26), and goes on to argue that those assumptions have inherent problems. Others have found "... no demonstrable chaos in the time flow of quantum systems" (Ford 1989:367), while Popper (1972:215) and Prigogine and Stengers (1984) argue for indeterminism in quantum systems. So, with opinion going both ways, whether there is real chaos or whether what is seemingly "chaotic" is called chaos because of our inability to measure the motion of an electron (the Heisenberg uncertainty principle demonstrates the

inability to measure both the position and momentum of an electron without affecting one of these) once again appears to be the central problem to be resolved in establishing where validity lies in the determinism/indeterminism dispute.

Within chaotic systems there is usually some degree of stability. Turbulence within a river may be unpredictable with some particles of water moving upstream (the circular movement of water in eddies results in some particles moving upstream for short periods). Yet the river has as an "attractor", the force of gravity which draws the water down the slope of the river bed. While the movement of water particles may be incalculable in the short term, in the long term the particles will move downstream. Stable systems, where there is movement towards an attractor, can appear chaotic in their finer movements. The effect of these attractors has given rise to the term "deterministic chaos" (Coveney 1990, Mandelbrot 1990). Batterman, though, suggests that "it is unfortunately easy to be led by a failure of predictability to an erroneous conclusion about the existence and presence of genuine randomness" (1993:44). A system that may appear chaotic in one reference frame may be predictable from another.

Biologists such as Ernst Mayr are impressed by the physicists' claims of indeterminism:

This kind of uncertainty (Heisenberg's principle) is now so well known, as well as Bohr's complementarity principle, that I need say nothing further about it. What is often overlooked, however, is that one encounters even greater indeterminism when one moves from the study of unit processes, involving single entities, to that of larger systems. Whether one is dealing with ocean currents, weather systems, or in cosmology with nebulae and galaxies - all of them purely

physical systems - everywhere one encounters strong turbulence, due to stochastic processes that preclude the making of strict deterministic predictions (1985:48).

Mayr's reference to indeterminism is entirely human centred. He uses indeterminism from a human reference frame to imply that there is a fundamental indeterminism, that is, an indeterminism from all reference frames. I believe this is a mistake; a consequence of the tendency for non-physicists to be misled by the enthusiasm of some physicists. There is certainly much within our world that is difficult for us to predict, such as earthquakes, volcanic eruptions, bodies colliding with the earth, and so on, but this does not mean that they are indeterminate from *all* reference frames. Because we cannot predict an event only demonstrates that it is indeterminate from our reference frame.

John Maynard Smith recognised this difficulty in defining randomness. He wrote, "perhaps the hardest concept in science for most of us to think about is that of randomness" (1981b:201). And his solution: "... it is sufficient that a scientist, by treating some set of events as random, is asserting that there is no structure in these events which is relevant to the phenomena he is attempting to understand" (1981b:204). I will adopt the position of Batterman and Maynard Smith, that is, while there is indeterminism from the human reference frame, to extend this to imply a general indeterminism cannot be justified at this stage.

The term "reference frame" is synonymous with the term "eye-view". I will later refer to a gene's "eye-view" and a meme's "eye-view". In the tossing of the coin, the computer "knew" the outcome regardless of whether a person was reading the computer's calculation or not. We could say that, from the computer's eye-view, the outcome of the toss was known. It may seem strange to consider the eye-view of an inanimate object such as a computer, but Dawkins (1976) uses such

expressions as “a gene’s eye-view” to argue for selfishness from the perspective of a gene. The gene has a real experience of its environment, particularly in its role of promoting certain chemical reactions within a cell.

An organism, in its interaction with its environment, is selectively advantaged by an ability to reduce the amount of indeterminism that it experiences from its eye-view. It will be argued later that the gene is the unit of knowledge through which indeterminism is reduced. Of two organisms, the one that can reduce indeterminism to the greater degree will be selectively advantaged over the other. Yet in saying this I am saying nothing about the determinism/indeterminism debate. This debate is whether there is indeterminism from *all* reference frames. If this occurs there is genuine indeterminism. Future references to indeterminism/determinism will refer only to the ability of an organism to “know” its environment from its reference frame.

An organism’s environment is, in part, indeterminate from its eye-view. An organism is advantaged by reducing that amount of indeterminacy. This reduces the randomness that an organism experiences and so allows greater control of its environment.

2.3 Exactness and Optimums

Earlier I argued for the uniqueness of every organism. Physical things also show great variation and it is unlikely that two objects have identical dimensions in respect to weight, temperature, and size. Consider the weight of two objects. A person holding them has an instinctive feeling as to their relative weights, but this is an internal perception, and even if they feel about the same weight he would not expect an accurate instrument to show them as equal. To argue this, consider two objects whose weights are measured to be the same at ten

decimal places (say). Would they be the same at one hundred and, if they were the same at one hundred, would they be the same at a thousand places (and so on)? As it cannot be shown with certainty that two apparently identical measurements will still be the same when a more sensitive instrument is used, proof of exact weight is clearly impossible. No instrument has the capacity for measurement to any chosen number of decimal points. Thus, regardless of the sensitivity of the instruments used for measuring, the exact weight of an object can never be known. To my knowledge, no proof exists that even two fundamental particles, such as protons, are of the same mass. An object's weight, then, can only be known to the degree of accuracy provided by the measuring instruments available. The weight, if it is in fact constant, can never be known.

The background gravitational flux (Will 1989) that we are constantly with (reverberating from the initial "big bang"), as well as the changing gravitational flux from the movements of the planets, creates a weight flux in objects. Although this variation is admittedly very small, it is sufficient to demonstrate the inexactness of weights. Weight is a flux, continuously changing with time.

The same argument can be made with length. If a metal rod of one metre length is heated, then as the metal expands it will be longer than one metre, and if the rod is then cooled to a temperature less than the original, it will be less than one metre. As the rod cools it must be at some stage exactly one metre. If the rod's length has changed from 1.1 metres to 0.9 metres over a time of one minute, for how long was it exactly one metre? For simplicity, assume the rod shrinks at a constant rate with time. Let the time for which the rod is exactly 1.0 meter be T seconds. As the rod shrinks at a constant rate, it must also have been T seconds at 1.05 and at 1.0500078 and so on; in short, for any numbers within that range. For any finite range there is within this range an infinity of different numbers. However the total number of numbers

multiplied by T should give one minute. But infinity multiplied by T seconds is infinity, leading to a contradiction. T can then only be zero.

The idea that an event can happen for zero seconds seems an anomaly that needs further explanation. These anomalies invariably arise in mathematics where the concept of infinity is employed. Consider a clock that shows five minutes to twelve. Ten minutes later, as we would expect, it reads five minutes past twelve. Over this period there are infinite times, one of which will be exactly 12 o'clock. The length of time during which it is 12 o'clock is zero seconds, just as the rod's length above was exactly one metre for zero seconds. To argue this, the ten minutes can be progressively divided into ten divisions of one minute or one hundred divisions of 0.1 minutes or one thousand divisions of 0.01 minutes and so on, so as to approach infinite divisions of zero seconds. At infinity the time of a division is zero. This example indicates the continuous nature of our world in time and space, although matter may be thought of as particulate at the level of the atom. An organism's interaction with its environment can be seen as a continuum of events, each of zero seconds duration.

Imagine a series of measuring devices applied to our iron rod above, with each measuring device used having such features that enable it to measure with increased accuracy over the previous device used. Measurements taken are 1.1, 1.05, 1.06, 1.056, ... and so on. These are converging to some unknown limit. Yet for each measurement, say that of 1.06, it is unknown to the measurer whether the next measurement will be higher or lower than the current measurement. For the measurer who is unaware of the next value, 1.056 might just as well have been 1.064. From the measurer's reference frame, the new measurement is randomly above or below the previous measurement. This is no different from the tossing of the coin with the result of heads or tails (where heads is below the exact value and tails above, or vice versa).

We may measure two objects and get identical results. But this does not mean that the two objects are identical in respect to this value. It only indicates that the difference between the measured values is less than the sensitivity of the measuring instrument. A scientific experiment, repeated in order to check another's work, cannot produce *exactly* the same results as the original experiment, but measured results may be the same. The history of measurement is characterised by a progressive attempt to find greater and greater accuracy. For example, the development of the microscope started with the magnifying glass and culminated in the electron microscope. But an exact measurement is not always sought. The scientist seeks only that accuracy necessary for his purposes. The engineer who builds a bridge may use mathematical equations that approximate the stresses and strains in the materials, but still give an accuracy that guarantees the safety of the bridge. That is, an *optimum* is sought that lies between too great an accuracy and too little an accuracy. The engineer, for efficiency, must find that degree of accuracy that minimises time and cost spent yet produces a viable bridge.

In the previous subsection I suggested that an organism that reduced the indeterminism of its environment was selectively advantaged over another that did not reduce the indeterminism to the same extent. This must now be modified. The organism must not expend excessive amounts of energy to know any component of its environment to a greater accuracy than is necessary for survival. An organism need only know its environment well enough to survive yet, not so well that energy is lost in the acquiring of needless knowledge. The worm need only know of the bird's habits of eating worms and when and how it hunts. A worm does not need to know about the bird's courtship rituals or about the habits of rabbits. While this knowledge would increase in the worm's understanding of its environment, the knowledge would not

be advantageous to its survival. An organism then, seeks an optimal knowledge of its niche, where that optimum represents a level of knowledge less than an exact knowledge of an environment.

An organism is advantaged by reducing the indeterminacy of its environment, and in particular, those components of its environment that most affect its survival. Yet too much of an organism's resources and energy can not be expended in this process and the organism must seek, not an exact understanding of an environmental component, but an optimum that represents a lesser understanding. An exact knowledge of the environment can never be known.

2.4 Environmental Information

An organism interacts with its environment. It relies on its sensors (five for mammals; sight, sound, touch, smell and taste) to gather information about the environment through which it moves. All this could be called "environmental information".

A tree, the seed of which has fallen on infertile ground, may be shorter, with a more gnarled appearance than if the same seed had fallen in a fertile position. Had the seed fallen on a rock it may not have grown at all. Clearly there is a significant random component as to where the seed falls. The nature of the environment inherited, including random factors within that environment, can be seen as environmental information to the seed. The information a seed received in its descent from the tree determined its position of rest.

An amoeba probes its environment for food by extending its body. If no particle of food is encountered the amoeba may try in another direction. If food is encountered, the amoeba encloses the particle within its body and digests it. The "no food is found" or the "food is found" message

represent information that comes from the environment to the amoeba via its sensors. The animal assesses the information that is received and from this assessment, either continues with its current action or adopts a different action. Such things as water availability, fertility, location of food, presence of predators, and the activities of other organisms, all represent environmental information. Of two organisms, the one that can better assess its environment, and so reduce indeterminism, will be selectively advantaged.

Not all environmental information that is available to an organism is used. Just as the engineer did not calculate an excessive accuracy for the bridge, it is inefficient for an organism to assess environmental information needlessly. The worm need not know about the habits of rabbits; it is selectively advantaged in seeking that optimum between too little knowledge and too much. Here the habits of the rabbit represent environmental information, yet it is information that is not of interest to the worm. However the information "a bird feeds during the day" is of great interest (in terms of survival) and the worm will adjust its above ground activities accordingly. Environmental information is of differential use to the organism.

Sunlight is also information. For humans, from a wide spectrum of electromagnetic radiation (a product of the sun's nuclear processes) available, only a short band is used (visible light). This band is most common during daytime. Nocturnal animals process more infra-red light giving better night vision. The light captured by the human eye is reduced in accuracy through rod and cone cells with the cells firing or not depending on the average density of light on them. While the precision of the image can be increased by increasing the number of light receptive cells and/or increasing the size of the eye, this increase in accuracy may be unnecessary for survival. That is, the current level of processing represents the optimum that is most efficient. The eyesight of

birds is much superior to human eyesight as they specialise in capturing animals with precision flight. For humans this degree of precision is unnecessary in terms of survival and may even represent a waste of resources to produce it. Organisms use electromagnetic radiation in a way that enhances their survival. An organism might be disadvantaged by spending too much of its time and energy in trying to perceive its environment too exactly. Light detection is not new. Every stage of development, from the light detecting spots of the paramecium, to the mammalian eye, can be seen in one organism or another. The light represents environmental information to an organism, and detection of it reduces the randomness of its environment.

Organisms have little choice in collecting other types of information. They cannot avoid gravity, time, dimension, magnetic and electric fields, and atomic forces. These are part of our physical inheritance. The physical form of the Earth is environmental information. The non-linear relationships between dimensions is crucial in evolution. Consider the heat loss of an organism. The amount of heat generated by an animal is proportional to its volume, and its level of heat loss is proportional to its surface area (approximately). A cube of edge length L has an area proportional to L^2 and a volume proportional to L^3 . The ratio of heat loss to surface area can be given: Heat loss/ Heat gain $\propto 1 / L$. The smaller the animal the more it is susceptible to heat loss. To survive it must compensate for this heat loss with better insulation, or else modify its life in such a manner that the heat it does lose is not critical to it. In this case, the insulation or life style of the animal is related to its volume/surface area ratio. Large animals have an advantage in cold areas and small animals have an advantage in warm areas. A similar case to heat loss, can be made for the diffusion rates of oxygen taken into an insect's body. Air diffuses down trachea (tube like structures that are open at the surface of the insect and radiate throughout the body), with the diffusion

rate proportional to the cross sectional area of the trachea. However the oxygen requirement for metabolism is proportional to the volume of the insect. Because of this insects are limited in size of no more than a few centimetres in thickness.

The size of an animal in relation to its bone structure is also a consequence of dimension. If the cross sectional area of bone is proportional to L^2 and the volume proportional to L^3 , and if an animal was to grow to three times its original height then its bone area, and so bone strength, will increase by 9 times and its volume by 27 times. However this is now out of proportion; for consistency, the bone strength should also increase by 27 times. As Maynard Smith observes: "Larger animals are not geometrically similar to small ones; they have relatively stouter bones and very large mammals stand with their limbs straight, and are not flexed and so exposed to bending stress" (1968:7). The largest mammals, then, are to be found in the sea as they could not be supported on land. There is an upper limit to the size of terrestrial animals. The heavy bones of large animals, such as elephants, significantly affect their body form and habits.

Dimension, the Earth's size (and so the strength of gravity), and the Earth's chemistry (for example, a stronger chemical bond will make bone stronger), are the main selecting factors for form in animals. All constitute environmental information. Organisms that have evolved under these conditions have become attuned to it. They have a sense of time and space; properties of the Earth such as night and day have become an integral part of an organism's makeup (see Shepard 1989). The physical form of our world is like a mould that constrains organisms to certain forms, with that form depending on the niche it occupies.

Information received by an organism's sensors could be considered environmental information. As well, the characteristics of the earth and the

sunlight that bathes it are also environmental information that significantly determines an organism's form.

3. Genetic Knowledge

3.1 Introduction

This introduction will give a broad outline of evolution theory with this outline discussed in detail in the following subsections.

As argued earlier, an organism is advantaged by reducing the indeterminacy of its environment. "any living system accumulates information about its environment or, at least, certain properties of this environment. ... to this extent the life of any organism - be it a bacterium or *Homo sapiens* - is an information increasing process" (Wuketits 1988:457). Species progress in their *knowledge* of their environments through selection removing those organisms of inferior knowledge.

'Knowledge' is commonly used by humans to refer to their mental knowledge. It is an assured belief, instruction, enlightenment, learning, or practical skill. Can this term be used for animals without a brain? A plant acts on its environment and responds to variations in this environment: it grows, reproduces, respire, resists insect attacks, and so on. These acts are not random, but purposeful and controlled by the genes of the plant. The plant need not be conscious of them, but the acts are real enough. Through its genes the plant 'knows' something about its environment. Konrad Lorenz recognised knowledge in non-mental animals:

... the slipper animalcule (*paramecium*), which, when it meets an obstacle, first recoils slightly then swims on again in a random direction, 'knows' something quite literally 'objective' about its environment. ... The paramecium 'knows' only that the object is blocking its progress in the original direction, but

as 'knowledge' this will meet any criteria which from our own infinitely more complex, more sophisticated standpoint, we are able to apply. We might often suggest directions that the paramecium could follow to better advantage than that which it haphazardly chooses, but *what* it 'knows' is absolutely correct - namely, that it cannot go straight ahead (1977:6).

Having no brain, the knowledge of the paramecium can only be in its genes and it is these genes that produce its structure, direct its metabolism, and drive its actions (this knowledge also includes the DNA and RNA of the cytoplasm). I will refer to this knowledge within RNA and DNA as *genetic knowledge*.

Evolution is not a physical property such as a gravitational force or a magnetic field that directs or influences the behaviour of matter. Rather it is a name for a process, a process of the differential survival of offspring. While a tree may produce many seeds only one on average (over a long time period) will survive. Should this average be greater than one, the tree will soon dominate the landscape and, through crowding, bring the average back to one. Should the average be less than one then the tree will go to extinction. The change from many possible offspring to the survival of a few, is the process evolution. However, it would be wrong to say that evolution *caused* some trees to survive and not others. Only physical and chemical processes (including those of organisms) can cause things to happen. Evolution is not a causal process. What caused only one seed to survive was a combination of its genetic properties, and the environmental information received by it. The other seeds failed through either possessing poor genetic knowledge and/or encountering harsh environments.

If a genetic mutation allows one seed a better knowledge of its environment then it is more likely to survive over other seed of poorer

knowledge. These variations then accumulate within the gene pool. The genes represent knowledge of ancestral environments. An organism's current genetic knowledge represents a phylogenetic history of some past successful variations. By default, all of an organism's ancestors have reproduced at least once. Included here are not just members of the same species, but every ancestor back to the first life form. Naturally, many ancient genes have been lost in later different environments. On the other hand, many ancient genes have survived, as is evidenced by the common underlying structural patterns which characterise phylums.

Ancient genes can be found particularly in those environments that have been most constant. These may be restricted in range to certain micro-climates (such as the anaerobic environments of bogs). The rate of change of genetic knowledge will depend on the strength of the selection pressures acting, with this selection pressure coming from changing environments. Evolution is a knowledge process that "chases" changing environments.

If genes are a knowledge system, then an organism, such as a worm, can choose certain actions over others through this knowledge. It may seem unusual to talk of a simple organism such as an earthworm "choosing" a particular action. For humans, the word implies a mental choice. However this word does have real meaning in its application to the behaviour of a worm. In its movements through the ground it will prefer some locations over others. It chooses these locations, not through mental knowledge, but through genetic knowledge. The choice is made through knowledge gained by selections in past environments. A worm has *intention* through its genes. It is the intention of the genes to produce a certain structure, ingest soil, prefer some environments to others, and so on. Similarly with "belief". An organism has a genetic belief. If a worm restricts its movements above ground to night time so as to avoid birds, then it "believes" genetically that at this time it has greatest safety.

Worms that “believed” in daytime movement have all been eaten. The worm has a genetic knowledge of its environment and these represent a set of beliefs about that environment. Reasoning is at the genetic level and “new ideas” come through the mutation of genes and the differential survival of the consequent variations. Changes in intentions and beliefs are restricted to the generation length of the worm. The worm’s beliefs and intentions are fixed for its lifetime.

Of the two words, “information” and “knowledge”, either could have been used in referring to genes. I will use mainly “knowledge” as it is a more passive concept than information. Not all of the information within the genotype informs. Some may never be expressed (for example, recessive alleles). It is knowledge that the individual has, though it is not active.

Evolution is a process that reduces the indeterminacy of an environment for an organism through knowledge stored genetically. Words such as “intention” and “belief” have real meaning in a genetic sense.

3.2 The First Life

Life is usually held to have a number of characteristics. These are: structure (for example, cells are structured with membranes, proteins, mitochondria, DNA, and so on); response to stimuli and movement; growth; reproduction; respiration; and adaptation to changing environments. How did such life forms originate? There is every indication that this process began on Earth, in a “soup” of chemicals, commonly known as the primordial pool. Certainly most scientists seem to hold this belief. Of course, the prominence of this belief hardly constitutes a proof, nor should it. The evidence of life having evolved is not trivial with extensive records of the evolution of organisms in fossil records. I will assume life evolved in some primordial pool.

The original atmosphere on earth was a reducing one, containing the four basic elements (carbon, hydrogen, nitrogen and oxygen), and it was the interaction of these elements plus sources of energy such as atmospheric electrical discharges and electromagnetic radiation that led to the formation of the more basic organic molecules that are necessary for the living organisms of today. Processes such as rain brought these products down from the atmosphere and therefore away from their region of creation with its disruptive energy discharges. The first hydrocarbons, dating from around 3100 million years ago, resulted from the normal operations of physical and chemical processes (Calvin 1969). These hydrocarbons represent pre-organic life.

In the resulting primordial soup chemical reactions eventually led to amino acids forming. There are some 170 amino acids today with 20 or so making up proteins (a chain molecule consisting of a backbone of peptide linkages between successive amino acids). Only four are found in DNA. When polynucleotides (a polymer formed of purine or pyrimidine bases linked with phosphoric acid) came to be formed, and when these polynucleotides acted as templates for the synthesis of further nucleotides, the requirements of life were fulfilled. As Maynard Smith has argued: "We shall regard as alive any population of entities which has the properties of multiplication, heredity and variation" (1993b:109). Polynucleotides, could, if they acted as templates to reproduce further nucleotides, fulfil the properties of multiplication, heredity and variation and so be living. This requirement is more general than the traditional definitions of life given above. Growth becomes the few chemical reactions needed to produce a polynucleotide. Respiration becomes the energy needed for these chemical reactions. *I will accept in this thesis Maynard Smith's definition of multiplication, heredity, and variation as being properties that characterise life forms.*

The developmental basis for the first cells was probably RNA (Mason 1991:254). Such single celled organisms would have derived their energy by reducing sulphates and nitrates that were in the atmosphere. These types of anaerobic organisms still exist in environments of low oxygen, such as in the ocean depths or around the sulphurous atmospheres of volcanic vents. Other anaerobic bacteria (such as those that live in marshes) ingest hydrocarbons but, due to the absence of air, the breakdown is incomplete and products such as methane and hydrogen sulphide result, rather than the usual water and carbon dioxide produced by aerobic organisms.

Viruses consist of nucleic acid (either RNA or DNA) with a protein or protein and lipid coat. If the traditional tests for life given above (for example, do viruses respire, do they respond to stimuli?) are used for viruses, they would probably fail as a life form. However, by Maynard Smith's definition, they are living. The most widely held view amongst biologists as to the origin of viruses is that they came from active fragments of singular and multicelled organisms rather than being precellular entities (Morse 1992:218). In this case it is hard to imagine that an entity capable of self reproduction and the product of a living organism is in itself not living.

Where, then, is the boundary between the living chemicals (such as polynucleotides) and the dead chemicals that preceded them? This would be difficult to find as there are always intermediate forms that fall into both categories.

The first celled structures were prokaryotes such as bacteria and blue-green algae. They are haploid (a single set of unpaired chromosomes) and have a primitive nucleus. They are the evolutionary ancestors of the eukaryotes which are generally diploid (the chromosomes are in pairs). The eukaryotes have a true nucleus. These types of cell make up the

fungi, plants and animals. There are four nucleotide bases commonly found in eukaryotes, two purines (Adenine A and Guanine G) and two pyrimidines (Thymine T and Cytosine C). These four amino acids, in varying combinations, make up the DNA (there are up to six in RNA) of the nucleus. The fact that all eukaryotes have just these four amino acids suggests a common ancestry for plants and animals. Evolution has taken place by a combination of new messages (different arrangements of the same amino acids) rather than by the addition of new amino acids. The new arrangements represent new genetic knowledge and the common ancestry is phylogenetic knowledge.

Another characteristic that points to a common ancestry is that in most organisms, the principal components of protoplasm, particularly the amino acids, are represented exclusively by left spiralling isomers. Yet in the artificial manufacture of these compounds equal proportions of left and right isomers are found. All life may have originated from left spiralling RNA.

Something is living if it has the properties of multiplication, variation and heredity. Replicating chemicals were the first life.

3.3 Genes

Segments of DNA have been labelled "genes". For example, a phrase such as "the gene for red wings in *Drosophila*" refers to that segment (or segments) of the fly's DNA that codes for this phenotypic trait. (I assume here that "red wings" is a genetic characteristic and is not caused by some environmental influence in which it grows.) The exact position of this segment may be unknown, however the term "gene" is still a necessary one. A gene is generally taken as a length of chromosome concerned with making at least one polypeptide chain (many amino acids linked together by peptide bonds). It can be considered a unit of

inheritance that codes for a particular characteristic in an organism. All the genes of an organism represent its genotype, its genetic knowledge. The physical and behavioural characteristics of the organism constitute the organism's phenotype. Unlike the genotype, the phenotype varies throughout the life of the organism. It is influenced by the environmental information with which the organism develops and lives.

Human DNA and its functioning is poorly understood. A current area of research is to map the sequences of amino acids in DNA. Stebbins and Ayala, for instance, also note this lack of clarity and the apparent self-serving behaviour of genes:

Segments of DNA with no known function have been found in surprising numbers. In the human genome a sequence called Alu that is about 300np (nucleotide pairs) is present in some 300,000 copies, corresponding to 3 percent of the total human DNA. ... the discovery of these seemingly meaningless repetitions led to the speculation that some molecular evolution is deterministic, proceeding in a particular direction that is independent of chance and natural selection. Such sequences are held to have multiplied not through a series of random events but because a kind of "molecular drive" impelled each sequence to reproduce itself within the genome (1985:55).

The idea that genes may put their own interests above those interests of other genes or the organism as a whole, is the subject of Richard Dawkins' book *The Selfish Gene* (1976). If genes have a "molecular drive" to reproduce for the *sake* of reproducing then it would explain how some DNA is carried without it corresponding to, or influencing a particular character in developing the phenotype. From this gene's eye-view it is advantaged by replication, even though the replications have no

phenotypic expression (Doolittle and Sapienza 1982, Orgel and Crick 1982).

The conventional view of evolution has all the knowledge for construction of the next generation contained within the genes. Variation occurs in these genes through mutation, and these variations result in differences in subsequent phenotypes. However, there is evidence of at least some transferral of information from RNA and also from proteins to DNA (Mason 1991:251). This seems more an exception to the rule than a general trend. It is yet to be investigated thoroughly. Lamarck (Huxley 1964) claimed that acquired characters could be inherited. To demonstrate that Lamarckian inheritance is relevant in a genetic sense it is necessary to show that a characteristic acquired during an organism's lifetime can be passed to an offspring through the genes. For inheritance, an acquired characteristic would have to be passed to the germ cells (sperm or ovaries) and so transferred to the next generation. If RNA or proteins can transfer their code to DNA within a gamete then this would constitute Lamarckian inheritance. This process has yet to be demonstrated, and any confirmation of it would complement evolution theory rather than contradict it.

Cell chemistry is poorly understood. DNA is not exclusive to the nucleus of a cell. Organelles within the germ cell such as mitochondria contain RNA and DNA which is also subject to mutation and inheritance (Asmussen and Schnabel 1991; Schnabel and Asmussen 1992; Pooni *et al.* 1991; Vaidya *et al.* 1993). In mosquitoes, the cytoplasm contains genes which are inherited on the maternal side and these genes bias the male/female sex ratio by killing the male embryos (Hurst 1991). For change, a mutation can occur in the cytoplasm of the germ cell in the maternal line. While the ovary contains cytoplasmic DNA, the sperm contains little or no cytoplasm at all, having only nucleoplasmic DNA. The mutation here is still a random process not acquired through the

usefulness of some phenotypic trait. This gene transmission could be thought of as asexual reproduction in the maternal line. The full cytoplasmic DNA complement is inherited. Sexual reproduction could thus be thought of as having a small asexual component. In these cases inheritance is still genetic. There is no Lamarckian inheritance in the asexual component.

There are other possibilities of Lamarckian inheritance that do not need acquired characteristics to be encoded on resident genetic material within a germ cell. Acquired characteristics can go into the germ cell in *any* form. Research has shown that the cell may contain foreign genetic material in the form of viruses or infectious proteins (prions) that are transmitted to offspring (Wickner 1994). In this case the inheritance may be Lamarckian. An acquired characteristic, genetic material that has invaded the cell during the lifetime of an individual, has been passed to offspring via DNA, RNA or protein stored within the germ cell.

A further possibility of Lamarckian inheritance is an acquired characteristic passing, not into the germ cell, but into the developing embryo. For example, the transferral of antibodies acquired by the mother to her offspring through her placenta, or through her breast milk, appears to be the passing of an acquired characteristic.

Overall, knowledge is passed to the offspring through the germ cells, with that knowledge not restricted to nucleoplasmic DNA. As such, the term "genetic knowledge" can be broadened to mean *any* unit of cellular knowledge that is capable of inheritance.

Genetic knowledge, in tandem with environmental information, generates both structure and behaviour that defines the phenotype. It may appear that this knowledge plays little part in coding for the behaviour of animals with brains. However a study of sheep dogs

demonstrated that most behaviour in these animals was through genetic knowledge. One particular type of European dog lived with the sheep herd and its presence inhibited attacks by wild dogs. Through human selection on the neotenous playful characteristics of juveniles, the onset of adult predatory behaviours was arrested. The sheep dogs therefore had their normal aggressive characteristics towards non-conspecifics eliminated through selective breeding (Coppinger *et al.*, 1987). Such processes emphasise the role of genetic knowledge in behaviour.

In humans Piaget (1973) noticed that children are consistent in the sort of errors that are given for a specific age. For example, two identical glasses with the same amount of water in each are emptied into a long tall glass and a short wide glass. Children up to a certain age (about 5) believe that there is more in the tall glass than the short glass, even though they previously agreed with the conductor of the experiment that the amounts in the original glasses were equal. For children, a sense of quantity develops in later years. Similarly, Chomsky (1976) considers there is to be a fundamental underlying structure common to all languages; a genetically driven grammatical structure. The natural musical ability that some children show at a certain age also demonstrates a strong genetic content for this talent. Genetic knowledge underlies much of human behaviour.

The knowledge a bird has of how to build a nest is also genetic. A bird reared in an empty cage may still make movements as if to make a nest. Similarly, the drive to stalk and catch mice still exists even if the cat is surrounded by many mice. In order for the cat to satisfy this genetic urge the cat "... always chose those [mice] farthest away in the opposite corner of the room [to stalk], and ignored those that ran over its fore-paws" (Lorenz 1966:78). Genetic drives may thus initiate behaviours regardless of the environment of the animal. Observations similar to these have led

to the development of a theory of genetic epistemology (see Hooker 1994).

The term “gene” can be considered as any unit of knowledge that is passed via the germ cell. The interaction of this knowledge and environmental information produce the phenotype of the organism.

3.4 Fitness

In the following sections I will consider the meanings of fitness, selection, and adaptation, acknowledging at the same time that it is difficult to discuss one without making references to the others. To minimise this problem I will give a brief definitions of each in the next paragraph that will serve until these terms can be considered in more detail.

Darwin used the term “fitness” to mean “well adaptedness.” Of two organisms, the one better adapted to its environment has greater fitness. Darwin’s “natural selection” is a process of the differential survival of organisms in their environments. This results in the elimination of individuals whose adaptations (traits) are inferior to other animals. An organism receives information from its environment through its sensors. It then chooses actions depending this information. The more successful the actions chosen, the greater is the organism’s fitness. An organism that fails in its environment could be seen as being selected against by that environment. An adaptation is a characteristic of an organism that assists survival in some environment.

Organisms vary in fitness due to genetic differences and differences in the environments they encounter throughout their lives. In asexual organisms, all the offspring are genetically identical with the parent (except for mutations) and so have the same fitness in terms of their genotypes. However offspring may have different phenotypes due to

their experience of different environmental information. The range of phenotypes of the offspring indicates the environmental variation.

For sexual organisms, variations in offspring are more pronounced due to the effects of DNA splitting and its recombination. Here variation is not solely dependent on mutations. Human children are distinct from their parents yet no mutations need happen. Such is the variation in some sexual organisms that it is not strictly correct to speak of "reproduction" as neither parent is reproduced (Keller 1987). Genetic variation and environmental variation, both affect the likelihood of an organism's survival. Using an earlier example, a plant's seed may fall on fertile ground with the seed's survival almost assured. In contrast, the same seed may fall on rocks or in water allowing no chance of growth at all. The seed appears to have little control over this random element. But, as argued earlier, an organism is advantaged by reducing the indeterminacy of its environment. The tree seed may be advantaged by having various wings, hard coverings, hooks and so on, that reduce its chance of falling on bare rock, or if it does so fall, helps it to move to another more suitable spot. These features represent additional genetic knowledge. In this way the randomness can be reduced but not entirely eliminated. Such reductions in randomness (indeterminism) could be seen as increasing an organism's fitness.

However, fitness is a very vague term, not helped by random components that persist in any environment. A number of attempts have been made to define more precisely what fitness means. Byerly and Michod (1991) divided fitness into two types, one based on a genotype's actual rate of increase, excluding randomness, the other based on environmental factors with which the organism systematically interacts, including randomness. Yet such definitions appear too contrived and fail to account for fluctuations in both randomness and the environment. The environment, as a flux, and as a component of any animal's fitness,

means that any fitness value is also a flux. Other definitions also fail. For example, it could be argued that some organisms have a *propensity* to survive (given a particular environment) over others (Mills and Beatty 1979, Waters 1986). Here fitness is independent of actual survival or production of offspring. It is a property of an organism. This is an alternative way of determining fitness to the usual "number of offspring" produced. Under this definition, an organism that eventually produced no offspring may have originally been classified as having greater fitness than an organism that produced many offspring.

Defining fitness as a *property* of an individual ignores the environment of that organism. The same organism may be born in a number of distinct environments. Its fitness in one of these environments may be clearly higher than in another. Here it could be equally true to say that the fitness of an organism is a property the environment it is in. One type of environment may be more suitable to the character of one offspring than its brother. A climate change through desertification, rising sea levels, or continental drift, will cause long term physical changes. With change, different selection pressures come into play. If environmental changes that an organism experiences are a function of time, then so is fitness a function of time.

Another form of fitness is "inclusive" fitness. This term is more useful. A lioness that is left in charge of a pride's cubs, while the other members hunt, is increasing her inclusive fitness by helping those cubs. It is more than likely that she has sisters or brothers in the pride and so by assisting the cubs of others, genes she shares in common with the cubs will be selectively advantaged. It is in her genetic interest to care for those cubs irrespective of whether she has cubs of her own. A childless person whose kin have children while he does not, has still reproduced some of his genes through his kin. It is in his genetic interest to assist in the survival of those related offspring. To do so increases his inclusive

fitness. The argument of inclusive fitness is often used to explain the sterility of workers in social insects. Sterile worker bees, by assisting in the rearing of the offspring of their genetically identical parent, the queen bee, thereby assist with the proliferation of their own genes. The worker has an inclusive fitness even though it will never reproduce.

“Fitness” is more useful as a general term for comparison between organisms. For example, it is clear that a deer with a broken leg is less fit than one without. Yet to quantify fitness values for less extreme cases would be an impossible task due to random components within an environment. The human environment is considerably more detailed than the environments of other animals. Few people would be prepared to predict with certainty a person’s likely survival and production of offspring. Very small environmental differences can have a profound effect on decisions made. Fitness is useful as a concept for comparison, but it otherwise has little practical application. I will therefore avoid the term “fitness” in this thesis, preferring instead to talk of an organism being “selectively advantaged” by one attribute over another.

Rather than talk of the fitness of an organism, it is more useful to nominate a specific structure or behaviour as being selectively advantageous or detrimental to an organism, in respect to a particular environment. An organism that assists kin increases its inclusive fitness.

3.5 Survival of the Fittest as a Tautology

The phrase “survival of the fittest” has often been labelled tautological. Any person who takes the circularity of the “survival of the fittest” as indicative of a flaw in natural selection has failed to understand the meaning behind the phrase. Darwin’s (1859) original understanding of the process of “natural selection” is clear; better adapted individuals are more likely to survive over those less well adapted. The phrase “survival

of the fittest” as it stands today has two difficulties. First is the implied circularity. A fit individual is one best able to survive and so the phrase reduces to “survival of those best able to survive”. Secondly, the random element in evolution will in some cases select against those animals that are most fit. In this case “the survival of the fittest” becomes “the fittest are the most likely to survive”. Having the greatest fitness is not a guarantee of survival.

Another problem is that it suggests that there is a continuous struggle between an organism and its environment. Such a belief is mistaken. Expressions such as “nature red in tooth and claw” only apply to those “bottle necks” where there is shortage of food, nesting sites, mates and so on. To avoid competition most animals have their offspring during spring, a time of plenty. Abundant food allows leisure and play. For example, young lambs have a game, if there is a mound available, of “king of the mountain”. Each lamb tries to occupy the hill at the expense of the others. The lamb experiences real pleasure in doing this. While it can be argued that this pleasure is simply a reward for practising skills that will later be used more seriously for mating or defence, the experience of pleasure is undeniable.

A founding species will also experience little competition. As the niches available to it are unoccupied the species undergoes “adaptive radiation” and it breaks up into many species to occupy those niches. For example, Darwin’s finches on the Galapagos islands underwent speciation (see Ridley 1985, chpt 8), developing a wide variety of beaks for different niches. As the population density of animals reaches saturation, competition returns. A similar example can be seen after catastrophes. Imagine a drought that kills the majority of the organisms in an area. Good seasons return and it takes a number of generations for the population to build up to levels approaching the normal carrying capacity of the area. Organisms born after the drought would have no

knowledge of it and may complete their lives without ever experiencing competition (except possibly for mates). Every animal from a litter might survive here. In times of plenty it is not just the fittest who survive. All animals survive, both the well and the poorly adapted. This is a common situation in the fluctuation of rabbit numbers in Australia. Frequent droughts in some parts of the continent cause a situation of boom and bust in respect to rabbit numbers.

Even if the phrase “survival of the fittest” is judged tautological, as Gallagher (1989:20) points out, it cannot be open to falsification. It is simply a true statement that does not tell us anything, not one that is untrue. For example, the phrase “water is wet” is tautological, however it is not untrue, nor could its tautological nature be used to argue against the fact that water is wet. (Various fundamental religions use the tautological nature of “the survival of the fittest” as an argument for the falsity of Darwin’s ideas.) A self evident statement may not be informative, but it cannot be a false.

While the phrase “the survival of the fittest” may be tautological, this phrase is of no consequence to the synthetic theory. An organism’s experience of competition varies differentially over time. Periods of low competition allow play and leisure.

3.6 Selection

The characteristics of a niche represent selection pressures on an organism. The organism will fail if it cannot accommodate these characteristics. For example, saltwater is a characteristic that selects for organisms sympathetic to its form. A freshwater fish or a land animal may be killed in an environment of saltwater. The saltwater selects against them. Through these selection pressures species are drawn to forms that work in their interactions with their environments, that is,

they survive and reproduce. Sea fish do well in saltwater. Past selections have resulted in a suitable physiology. Certain characteristics of saltwater, such as its reflection of light, will select for dark colouring in the upper body of pelagic fish and light underneath the fish. The saltwater's corrosive properties will select for resistant membranes and mucuses that enclose the fish. An organism's form, through selection, becomes finely tuned to the environments with which it interacts.

The action of saltwater in selecting for certain characteristics in organisms is a "directional selection". This is a general term that encompasses all forms of selection. A desert environment selects for techniques to conserve water needs. The "artificial" selection by humans of plants and animals is a directional selection for these organisms. The surviving organisms have features more sympathetic to their environments, environments which contain humans. Any selection process promotes the survival of some organisms over others and so differentially changes the gene pool of that species. Such a change is directional.

Say there are two organisms, one that, through possessing certain genes, survives a disease while the other is killed by it. The genes that allowed survival could be thought of as having a "knowledge" of the disease. Through selection, knowledge about the environment, in this case the disease, will spread throughout the species. In this way numerous selections result in the "knowledge process" referred to earlier. A species becomes a phylogenetic record of past successful environmental interactions.

Directional selection processes may vary in strength. In a study of finches in the Galapagos Islands, Boag and Grant (1982) found that the intense selection during an extreme but uncommon environmental condition, drought, caused widespread change in bird species numbers.

Such intense periods of selection can have significant effects on species that are otherwise well buffered (able to adopt a number of strategies for survival) to the impacts of small environmental changes. Here the directional selection of the drought was such that the normal seasonal fluctuations of bird numbers were severe, sending some species to extinction. Humans are also part of the environment of animals and so a directional selection upon them. The hunting and poaching of elephants for their tusks is a directional selection for small tusk size (Jachmann *et al.*, 1995). The loss of native species in areas cultivated for food production and the death of species by chemical contamination of waterways, both represent strong directional selection pressures. Through selection there has been a loss of genetic knowledge.

In contrast, animals that colonise environments in which there are few selection pressures undergo speciation through "adaptive radiation". Here a species may experience little competition across a range of niches. A single colonising species radiates out forming new species that are specialised to particular niches. For example, the extinction of the dinosaurs resulted in a rapid speciation of mammals to fill vacant niches. There is a rapid increase of genetic knowledge in mammals.

In stable, well established environments, the directional selection can be "normalising" or "balancing". Through selection, harmful new variations are eliminated. Balancing selection tends to maintain existing forms. Genetic knowledge is kept constant with new genetic "ideas" failing. The saltwater crocodile has undergone little recent change and is a successful survivor. The stable environment that it occupies has allowed the crocodile a long time to become finely tuned to its environment. New variations are unlikely to be successful as any beneficial mutations have long since been included in the species gene pool. For humans living in malarial areas, balancing selection may maintain heterogeneity. Sick cell anaemia is maintained in the

population with heterozygous individuals being selectively advantaged over homozygous individuals. Indeed, the sickle cell allele in the homozygous form is often fatal to the individual. Over time the selection pressure of the malarial parasite has stabilised the frequency of the resistant allele. This stability can be upset if the environment suddenly changes through a physical change or an invasion by a new species. Strong directional selections will return in an unstable environment. If a disease for mosquitoes made the mosquito rare, then sickle cell anaemia allele would disappear.

Canalising selection (Waddington 1957, Dobzhansky 1970) is a type of directional selection that channels an individual's development towards particular forms, suppressing variation. A person may vary in size and appearance depending on the environment in which he is raised, however, constant features such as two legs and two arms always develop. These are genetically inflexible structures and represent "canals" down which development must flow (considered in detail in section 3.16).

Directional selection is a characteristic of all interactions of an organism with its environment, and applies to both larval and adult forms. Genes control larval development and the success of those larva will reflect on the survival of those genes. The environments experienced, and selection pressures from them, may be quite distinct for larvae and for adults. The selection pressures acting on an adult butterfly and those acting on the caterpillar are clearly different. The caterpillar must be able to digest various plants and escape predators living on and around those plants. An intermediate stage, the chrysalis, must avoid desiccation, detachment from its branch, and disguise itself from predation during its metamorphosis. The butterfly must avoid aerial predators, find a mate, and produce eggs. For a small animal, all this intricacy seems to be

asking a lot of the genes. Each stage could almost be seen as an animal in itself. Success of the species requires success in all stages.

Differential success of one stage over another resulting in the predominance of the successful stage, is often referred to as neoteny or paedogenesis. Let us suppose that the caterpillar experiences much less predation than the butterfly. A variation that resulted in a longer caterpillar stage and a shorter adult stage may be selectively advantageous. This may lead the adult stage to become progressively shorter and may even be eventually lost. The retention of successful larval features in newts and salamanders, the external gills, may be a case of this. It is quite feasible that the vertebrates have derived from selection pressures on the larval stage of the Urochordata (sea squirts) (Hardy 1959, Young 1962). The sea squirt has a larval stage that is free swimming, and, if it became fixed in that form and able to reproduce, the adult stage would be redundant. Speciation would then be at the level of the larva rather than the adult. Humans, as vertebrates, may have evolved from the selection pressures on a larval form of the sea squirt.

While selection is an ongoing process it varies in strength. As argued earlier, it is the "bottle necks" of an organism's life that provide the strongest selection pressures. Irregular or seasonal food shortages, competition during breeding, predation and so on, all represent selection pressures. Characteristics of an environment differentially exert selection pressures on organisms. A bird is a selection pressure on a worm, yet a rabbit is not. Selection is for a genetic knowledge of those characteristics with which an organism interacts.

Selection can be on many levels causing different physiologies and behaviours. In a study of testis weight (Harcourt *et al.* 1982), gorillas and orangutans were found to have testes of about one quarter the weight of chimpanzees yet chimpanzees were lighter in body weight. This was

seen as a result of their breeding systems. In the gorillas and orangutans one male monopolised a number of females and there was no risk of infidelity. Each male only needed to ejaculate enough sperm to result in fertilisation. Chimpanzees, though, are promiscuous, with several males copulating with each oestrous female. A male's chance of success in fertilisation depends on the volume of sperm produced, with this sperm having to compete with other sperm within the female chimpanzee. In the orangutan and gorilla, selection for mating occurs at the level of the adult on the basis of such traits as physical size and strength. In the chimpanzee selection is at the level of the testes, through the volume and vigour of the sperm produced. Selection for mating has evolved here on two different levels. There are two distinct body forms (large and small testes) resulting in two distinct behavioural types. Similar results are found across a range of vertebrates including birds (Moller and Briskie 1995).

Many similar examples exist. In the Australian dingo, the dominate female of a pack may kill all the other pups of the other females. This infanticide is the main method of suppressing reproduction. While the structure and dynamics of a wolf pack is largely similar to the dingo, in respect to control of offspring numbers, the wolf pack is limited in size through the dominant female suppressing copulation (Corbett 1978). Two different mechanisms have evolved to restrict breeding to the dominant animals with this restriction occurring when resources are limited.

Organisms, through directional selections, gain a genetic knowledge of their niches. The knowledge of species will increase in speciation (adaptive radiation) and decrease with extinctions. In constant environments the knowledge of a species will stabilise through normalising selection.

3.7 Mutation and Randomness

Evolution is only possible because selection acts differentially on variations. These variations come from mutations within the DNA of the germ cells, with these mutations being expressed in the offspring. Variation in genes is through substitution, addition, deletion or inversion of nucleotides within a section of a chromosome. This is caused by such variations in the chromosomes' environment as electromagnetic radiation and chemical imbalances. Another possibility for mutation is genetic recombination (a rearrangement of linked genes as a result of crossing over during cell division). Some organisms, particularly some types of plants, undergo polypoidy which could also be considered a mutation: "... a doubling up of the number of chromosomes from one generation to the next, producing offspring that are usually reproductively isolated from the parent generation and in effect constitute a new species" (Stebbins and Ayala 1985:56).

A mutation in a germ cell represents new genetic knowledge which will be retained if the cell survives development. This knowledge has been gained within the lifetime of the new organism. For retention, the organism needs to be successful in reproducing. The mutation will then become part of the phylogenetic knowledge of the species. Mutations in those cells other than the germ cells, the somatic cells, cannot pass to the next generation. Here a mutation is unlikely to be beneficial. Should the mutation allow separate regeneration, then the organism's body may become a resource for that cell. For example, a human skin mutation (skin cancer) may result in independent breeding of that cell (see section 3.14), yet this mutation cannot be passed to offspring.

The usual role of genes is to produce the structures of the organism (such as red blood cells, bones and tissue), and to produce behaviours that allow interaction with the environment. Such behaviours are often

termed “innate”. However there is a second type of gene. These genes make enzymes that are responsible for replicating DNA and correcting errors in this replication. The enzymes required for this may have evolved initially to repair damage to DNA. As this replicated DNA is the genes themselves, the correction of errors (mutations) is, in part, under genetic control (Maynard Smith 1993a:183).

John Campbell makes much of this new type of gene. He argues that the fact of randomness in genetic mutation may not be so certain: “gene-processing enzymes make the genome far more fluid and dynamic than had been imagined earlier. They probably are the source of most of the genetic variability important for evolution” (1985:135). Here, “some genetic structures do not adapt the organism to its environment. Instead they have evolved to promote and direct the process of evolution. They function to enhance the capacity of a species to evolve” (1985:137). One might think that if enzymes controlled by genes contribute to change, then these contributions are still arbitrary, and so selection would still only act on random changes. If an organism is favoured by a certain type of mutation, this will also select for those genes that caused this change and so promote more mutations of these kinds. “Selecting for a change in phenotype generates an attendant selection for evolutionary directors that favours that particular pathway of change” (Campbell 1985:144).

From this one could expect that in periods of stasis where an organism is well adapted to the environment, a high mutation rate (as mutations are more likely to be unfavourable than favourable) is a disadvantage. In contrast, during periods of rapid environmental change, a high mutation rate would be of advantage as it may allow an organism’s offspring more variability and so the chance of at least some of them surviving. An organism, then, would be selectively advantaged if it could control the mutation rate within its germ cells. Organisms that occupy unstable

environments, or range over a number of niches, would be particularly advantaged by having such genes.

Yet even given that the genes control the rate of mutation, the mutations are still random. The genes may speed or slow the mutation rate but this does not imply a premeditated directional change. The increased variation within the offspring must still undergo selection and the remaining offspring will have features more sympathetic with the new environment. Indirectly, by increasing the variation in offspring, an organism more quickly evolves to a changing environment.

However, Campbell (1985) goes further implying that gene change is not random but directional. Change is to those genes that will improve the organism most: "sensory systems to convey information to genes abound in higher organisms, and some of these are known to control mutation, recombination, and the enzymatic alteration of complex genes in somatic cells. ... The crucial question for evolutionists now is not whether sensory evolution occurs, but how extensively prokaryotes and eukaryotes have recruited their sophisticated adaptive sensory systems to aid their evolution" (1985:148). Here I believe Campbell goes too far. I know of no evidence to suggest that directional changes are caused by genes. Although there are a few examples of the transfer of information from RNA and proteins to DNA (mentioned in section 3.3) this process is poorly understood. It is yet to be shown how information can be transferred to germ cells.

Organisms can engineer directional changes, but only through mating, not directly at the gene level. Sexual animals rarely mate at random but select mates. This selection may depend on such factors as the ability to perform a vigorous dance (in the fruit fly, *Drosophila*). Here a female has a chance to estimate the strength of her partner. Tests of strength are common in mammals, with the testing usually taking the form of direct

fighting or bluffing as two males compete among themselves for females. Females also seek males that appear healthy and fit. In some birds the magnificence of their plumage wins mates. Quail have a preference for first cousins rather than other siblings or distantly related individuals (Bateson 1989:289). Perhaps this cross is most vigorous. In mating then, genes do not mix randomly, but selectively. How an organism selects a partner can improve the success of its offspring. A genetic knowledge for partner selection is selectively advantageous.

Mutation is, in part, a random event in the germ cells and leads to variations in offspring. Genes may also control the rate of mutation, increasing variation in unstable environments. Some animals select mates that appear vigorous so as improve the genetic makeup of offspring.

3.8 Random Drift

An organism's interaction with its environment contains a random component. A random selection process results in "random drift". While the selection is random, it is still directional in the sense that the resulting gene pool is changed in a particular overall direction. Random selections could be seen as many directional selections with no overall consistency to that direction. I will use "random selection" to mean "random directional selections". In contrast, a directional selection driven by some constant environmental characteristic (such as saltwater), is consistent in its direction. Many small random selections may still result in changes within an organism if those random selections all add up to cause a net directional change. A useful analogy may be to think of a species undergoing many selections all of different strengths and different directions. If each of these random selections is thought of as a vector, then the sum of all the vectors may be significant. For example, say a species carries two alleles, one for dark colour and the other for light. If the colour of an animal has no effect on its chances of survival, then such

a trait would be considered selectively neutral. The levels of predation would be very similar for both colours. If the population size of this particular species is small it is quite likely that either the dark allele or the light allele will be eliminated, over time, by chance.

A simple experiment can be done to demonstrate this. Put ten balls, five red and five blue (say) into a container. Then select five at random and discard the other five. For example, three red and two blue balls might be selected. The selected balls are duplicated and returned to the container. There are now six red and four blue balls in the container. The process is repeated. One colour will eventually be eliminated, although the time required for this to happen will vary considerably. If, from the six red and four blue balls, five red are selected, the blue will have been eliminated. The ten balls could be ten animals that make up a small population with red being an animal with an allele for light colour and blue an animal with a allele for dark colour. The elimination of an animal could be through predation, and the duplication, through reproduction. One colour has been eliminated by chance. The smaller the population the greater the likelihood of the elimination of neutral alleles within the gene pool. Random drift will tend to decrease the volume genetic knowledge, particularly neutral knowledge.

The elimination of genes by chance, random drift, is considered to be a significant factor in evolution. This elimination will not necessarily result in the permanent loss of an allele. Random mutations are occurring all the time and these will continuously be added to the gene pool of the species. Many of these random mutations will be eliminated because they are harmful. Or, to put it another way, much of the new genetic knowledge will add little in respect to the organism's understanding of its environment (reducing indeterminism) and so will be lost. Other mutations are neutral or beneficial, and it is the neutral genes that are most likely to be lost through random drift. It is important to realise that

random drift plays a role in *all* selection, including the directional selection of harmful and beneficial mutants. For the red and blue balls, the colours need not be selectively neutral. Say red is chosen with a probability of 55 percent and blue with 45 percent. Balls selected are then replicated and returned as before. It cannot be assumed that the blue balls will be eliminated. Blue balls could still replace red coloured ones through random drift although this is much less likely than red replacing blue.

A mutation in a germ cell does not imply survival of that mutation. While a mutation in a germ cell may be for increased vigour, the adult that carries it will not have this increased vigour. The adult may be too old or incapable of reproduction. If the adult is successful in reproduction, the offspring with the new mutation represents a population of one. In the analogy above, it would be equivalent to there being only one red ball (say). Assuming the mutation is selectively advantageous, the red ball might have a fifty five percent chance of survival and it is most vulnerable here in to elimination. It may still be eliminated in the early stages through random drift. Once established, the allele should spread rapidly through the gene pool.

Random drift also applies to genes that determine the larval stages of organisms or genes that are responsible for replication of other genes (from the last section). After all, selection is throughout the life of an organism, so elimination at any one stage is critical for the species.

Darwin observed random drift in animals in the Galapagos Archipelago. Land tortoises, originally a single species that colonised the whole region, became independent species with different species inhabiting different islands. Here the environments of the islands were essentially the same. Species change occurred through random drift with the

elimination of enough genes such that breeding could not occur between different island populations.

Shanahan (1992) argues that selection and random drift are idealised concepts and represent terms for the extremes of a continuum of biological sampling processes. Of these sampling processes one is discriminating (directional selection) the other not (random selection). Interactions that seem to be completely random can still be found to have directional selection pressures. A lightning strike is often seen as a totally random event. But few people stand out in the open during storms. We instinctually avoid storms, although this may be more to do with the accompanying rain than possible lightning strikes. While a lightning strike is a selection pressure it does not mean that there is a genetic variation in some person that is knowledge "about" lightning strikes upon which this selection can act. These strikes are far too infrequent for them to be known genetically. On the other hand, a cheetah that succeeds in running down a Thompson's Gazelle, the genetic make-up of which resulted in it being slower than the other gazelles, would seem to be entirely a directional selection. Yet there is a random component in the cheetah and the herd of gazelles being together in the same place at the same time. A gazelle is also vulnerable in giving birth. Of course there is selection here as well, with those gazelles that can give birth more quickly, or hide their birth more effectively, or time the event to a period of low risk, having greater chance of survival. All interactions of an organism with its environment contain both directional and random selections.

The random selections encountered by organisms could be seen as a "white noise" similar to the white noise that forms the background of the output from devices that process electromagnetic radiation, such as televisions or radios. These random influences pervade every facet of life, making Darwin's theory of natural selection difficult to verify by

experimentation. Science usually requires an experiment to give the same results on repetition. If that experiment contains a random component the outcome may vary (with the degree of variation reflecting the strength of random processes). Due to this, the outcome may not be able to be repeated reliably. A chemical experiment (say) does not have this problem. When two chemicals are mixed and react to form a third, we have an experiment that can be reliably repeated. Clearly the results are not exact, but they are exact in the eye-view of the scientist, as his measuring instruments only have a certain degree of accuracy. Within this degree of accuracy, the two experiments seem identical.

Some authors have argued that all evolution (Lima-de-Faria 1988), or at least the most significant selective agent (Kimura 1983, Ho and Saunders 1984), is random drift. This is often referred to as the “neutral theory”. However, while most biologists see random drift as significant (particularly in small or isolated populations), directional selections make up the dominant *pressure* in evolution. Farmers witness genetically deficient animals die. Practical experience does not bare out the neutral theory. Maynard Smith (1993b:33) sums it up: “to explain the major features by species drift would surely be the ultimate absurdity”.

An organism experiences both directional and random selections in all interactions that it has with its environment. The component of evolution that results from random selections is referred to as random drift.

3.9 Adaptation

An adaptation is a structural or behavioural trait. It may or may not be selectively advantageous. A trait can evolve through directional or random selections or, most often, a combination of these. One form of selection may predominate over the other depending on the rate of

change of an organism's environments or the population density. The greater the environmental fluctuation, the stronger the selection pressures. Very strong pressures lead to death, or substantial death in a species, as that species cannot adapt at a rate that matches the environmental change. Humans compete with other animals for the same plant resource, by rapidly changing the environment of those animals. Take for example, spraying insect pests with insecticide for modern agriculture. The spray represents a rapid environmental change and so a strong directional pressure. Some insects may still survive and it is the genes of these that will predominate in future gene pools.

A shift in the contents of the gene pool may or may not involve mutation. Directional selection may act on an allele(s) already existing naturally in low frequencies. Such an allele may be selectively neutral and kept in the gene pool by random drift. An example often quoted is the industrial melanism of the peppered moth. Dark and light forms already existed before industrialisation but the dark forms were in the minority. After industrialisation, when the trunks of trees became blackened from air pollution, dark moths were better camouflaged while resting on the trunks, so there was a selection pressure towards dark forms with a corresponding shift in frequencies. A mutation was not necessary as the genetic knowledge that allowed the dark form was already present in the population (Kettlewell 1955). The frequency of alleles has changed. Here an obscure allele has come to dominate the gene pool, through a change in directional selection pressures caused by an environmental shift.

Evolution can occur through random drift. In the last section this was explained by analogy to coloured balls. Here the loss of selectively neutral genes can occur through random drift. From two sets of coloured balls, one colour may be eliminated by chance. A change has occurred without that change being an adaptation. The offspring that inherits an

attribute that is the result of random drift is not selectively advantaged through that attribute and so is not better adapted to its environment. Nor is it the case that all directional selections cause adaptations. The balancing selection that removes harmful mutations keeps species unchanged (as argued earlier for the saltwater crocodile). Populations will be kept genetically stable. Here selection works against new adaptations, particularly as those adaptations are inferior.

The fact that an organism has a particular adaptation does not necessarily inform us as to how that adaptation came to be there (see Resnik 1989 and Griffiths 1992). An adaptation may have come through a directional selection pressure in the past yet be selectively neutral in the present environment (for example, the human appendix). An adaptation that evolved for a past environment may be functional in the current environment, but serve a different purpose (called exaptation by Gould and Vrba, 1982). This is thought to be the path taken by the evolution of the bird's wing, with feathers once being an adaptation for warmth. Flight was a later adaptation to a different environment. Most birds still use their feathers for warmth and some only for this purpose, having again lost their power of flight (for example, penguins). An "adaptation" may be the result of random drift and be selectively neutral. I prefer "attribute" to "adaptation" as it is less suggestive of cause through directional selection. If all selection involves both random and directional components, then any adaptation has some degree of random drift in its formation.

Adaptations that do occur can only be additions or subtractions from existing features of an organism. A mutation that allowed a third arm for a human would be theoretically possible but from a statistical view point so improbable that it can be discounted. New mutations can only be small changes from the existing genetic structure. This does not mean that evolution cannot be rapid, for many small changes can quickly

create new species. But while an animal may benefit from a particular adaptation, this does not mean that mutations will occur that will allow evolution in this direction. Before any adaptations can occur, a species must "wait" for a mutation that leads to such an adaptation. This gene can then spread through the gene pool. For example, a cuckoo may lay an egg in another bird's nest of size and colour similar to the host. The host is unable to distinguish these eggs from its own (say). The cuckoo chick relies on a response to place food into a beckoning mouth for the feeding of the chick even though this chick may be unlike chicks of the host mother in both appearance and size. The host mother may not have the ability to recognise the impostor either in the chick or egg form. A mutation, new genetic knowledge, that allowed recognition of the parasitic cuckoo chick or egg, would be selectively advantageous to the host bird. Yet as such genetic knowledge does not exist, for the host bird the presence of the cuckoo could be considered just another environmental hazard. It is environmental information that is detrimental to the survival of the host similar to some random event such as a wind storm. Here phenotypic directional selection does not result in genetic selection. Yet once a mutation occurs that differentially advantages one bird over another in terms of resistance to cuckoos, then the cuckoo is no longer a random selection pressure, but a directional selection pressure.

In reality, the variety of hosts and parasitic cuckoos are many and varied (Hill and Sealy 1994, Lotem *et al.* 1995, and Sealy 1995). As the cuckoo egg becomes a better mimic of the host egg, the host in turn develops a greater ability to recognise the differences. There is then a form of "arms race" where the recognising ability of parasitic eggs and egg mimicry each lag the other. Host birds generally reject eggs rather than chicks although some hosts, such as magpies, learn to recognise their own chicks and will reject cuckoo chicks that are present in the same or later nestings. Clearly then, some of the recognition of cuckoo chicks is

through mental abilities and some through genetic knowledge. It is only this genetic component that I will consider in this chapter, the mental recognition will be considered in the next chapter as “cultural knowledge”.

Learning to recognise the cuckoo chick may not necessarily be of advantage. If imprinting is used for recognition, and the first chick raised is a cuckoo, then all further nestlings of the host will be wrongly rejected as impostors. This risk of the host not raising any of its own offspring may outweigh the risk of raising the occasional cuckoo (Lotem 1993).

A host bird would be selectively advantaged if it could reduce the indeterminacy of its environments through the accumulation of genetic knowledge of those environments (section 2.3). If a host bird developed a genetically driven behaviour that allowed a cuckoo egg or chick to be expelled, then the host bird would have reduced indeterminacy from its eye-view. Knowledge of the cuckoo would be incorporated into the species as phylogenetic knowledge. The host “knows” about the cuckoo genetically. The degree of randomness, that is, environmental indeterminacy, has been reduced.

Like the cuckoo, a disease that infects the organism, while there is no genetic resistance to that disease, can also be seen as a random selection pressure. It ceases to be random once a gene offering resistance allows differential selection of organisms with that gene. European colonists in places such as the Congo suffered from malaria as they had no genetic resistance to it. The majority of colonists died of this disease within a short time of their arrival (Weeks 1913). Resistance came not through genetic selection but from the use of quinine - cultural knowledge. The malaria itself represents a selection pressure, but if there are no genetic variations for resistance to malaria, resistance cannot be known

genetically. This disease was, before quinine, a random selection, not directional.

There are two possible reasons why organisms do not develop adaptations that are clearly selectively advantageous. The first is that mentioned above; the mutations that would allow a particular adaptation have not yet occurred. The second is that immediate stages are not selectively advantageous and so are lost. A gene that allowed a host to push at a cuckoo egg, yet not with enough force to expel it, would not be advantageous though one or more further variations may increase this pushing to the point where the egg is ejected. An insufficient push would waste the bird's energy and so such a gene would be lost. A similar criticism has been made by creationists against the evolution of certain features such as wings - how can half a wing evolve? Here the idea of exaptation is important; the wing undoubtedly had functions other than for flying in the past.

Some animals, not being favoured by mutations that would lead to beneficial adaptations, have utilised the genetic knowledge of other species that have the needed adaptations. For example, termites cannot digest cellulose directly yet this is their main diet. Some species of termites use cellulose-digesting bacteria living in their gut and then digest the bacteria, while others farm gardens of fungi, and the products of these fungi are then digested (Marasis 1971). The termites have indirectly adopted the genetic knowledge of the bacteria, effectively gaining the benefit of that knowledge. Humans have also utilised an array of single celled organisms in their gut to aid with digestive processes.

Adaptations are a response to environments. Similar environments will select for similar forms in organisms, even though ancestral forms may be different. The marsupials have developed a similar range of species to

the placental mammals yet the archetypes they developed from were different. The eye developed by the cephalopoda (octopuses, squids and nautili) is of a different structure to that of fishes, having evolved from a different archetype, yet it presumably underwent the same directional selection pressures as it lives in the same watery environment. Here similar genetic knowledge has evolved independently as a response to similar environments.

Another possibility is to evolve different adaptations to solve the same problem. Mammals in cold water may have fur or hair for insulation, as in the case of otters, or they may develop blubber as in some seals. Two different structures have overcome the cold. The mammals needed such a strategy, as, being originally warm blooded terrestrial animals that returned to the sea, they experienced problems with heat loss due to the higher conductivity of heat in water than in air. Sea animals, including fish, have a genetic knowledge of the sea temperature.

Adaptations are not necessarily beneficial. As argued above, they may have evolved in response to selections from an earlier environment and no longer be useful. If this is the case, it is likely that there will be an ongoing directional selection against this feature and that it will eventually be lost. An adaptation may be a disadvantage to an organism but be maintained in the population because the gene that codes for this adaptation is inseparably linked with another advantageous gene.

An adaptation may be maintained because the benefits outweigh the disadvantages. For example, the colourful plumage of a bird may make it more obvious to predators and also make it slower in escaping them. However the benefit of a colourful plume in attracting a mate might be greater than its risk of being caught. The evolutionary advantage of this trait is disguised by its multiple purpose. A trait will be selected for if the benefits to the organism outweigh the disadvantages. Selection is, of

course, for the organism's current environment, not some environment that may exist in the future. The Irish elk evolved a massive set of antlers and then suddenly disappeared (or so it would seem from fossil evidence). It is difficult to describe the significance of such an adaptation with absolute certainty. If the antlers were advantageous as a mating display, this advantage would need to have been greater than the disadvantage of carrying the excess weight. Whatever the reason, a runaway selection process seems to have taken the elk down a blind alley from which there was no return when a changed environment demanded it.

It is important to distinguish between adaptation and adaptability (Hahlweg 1991). If an organism is exposed to a changed environment, new selection pressures will act on it and the organism will either go to extinction or adapt to the new environment. Its ability to change to its new environment is a measure of the organism's *adaptability*. Generally, organisms that occupy a broad niche (generalists) will have greater adaptability than those occupying a narrow niche, one that may be highly specialised. The organism with a broad niche has inbuilt flexibility that allows variable behaviours. Such organisms could be seen as well buffered against environmental variation. In contrast, an organism that occupies a narrow niche, such as a gut parasite, needs less variable behaviours. A small environmental change could result in its death.

Acting against adaptability are directional selection pressures that eliminate adaptations that no longer benefit survival. For example, say two insect species, occupying roughly the same niche, colonise a cave. In this environment eyes have no function (say). If one insect loses its eyes while the other retains them, the former will be selectively advantaged. To make eyes takes energy, say one percent of an organism's resources. The insect with eyes will now have a disadvantage over the one without them. The insect without eyes has one percent more energy to devote to

other aspects of survival. One percent is significant in terms of competition and represents a “genetic cost” to the insect that retains eyes. Genes and the structures they code for that are a cost to an organism will eventually be lost. Yet in a variable environment this will not happen. If a cave is illuminated periodically, and during this time eyes are needed to escape predators, then eyes will be retained. This new environment is less specialised than before, needing a greater range of responses. Adaptability is thus a feature of organisms that have a broad niche; generalists.

Adaptations do not necessarily increase an organism’s likelihood of survival, even though the adaptation may function more efficiently thereafter than previously. It may in fact be less competitive if other species have evolved even better adaptive features that make them more competitive. To survive a species must change at least as fast as the other species with which it is in competition. The directional selection pressure for this change comes from competing species: “the Red Queen does not need changes in the physical environment, although she can accommodate them. Biotic forces provide the basis for a self-driving (at this level) perpetual motion of the effective environment and so of the evolution of the species affected by it” (Van Valen 1973:17; often called the “red queen effect”). Change does not necessarily guarantee survival then. Change must occur at least at the same rate as changes occur in competing species. If one species evolves faster than competing species it may force these competitors to extinction.

Adaptation is not to an exact knowledge of the environment but an optimum (section 2.3), that represents a lesser understanding of the environment. This lesser understanding is of lower genetic cost than a greater understanding and so selectively advantageous. For example, the evolution of the eye is not to an exact knowledge of the environment (perfect vision) but to a more functional reduced accuracy. An eye that

produced an image of great accuracy would require more of the body's resources and be selectively disadvantageous. It represents a genetic cost to the organism. A bird that builds a nest must not spend too much time in building that nest. While it could spend more time and make a better nest, this might be outweighed by the energy expended in doing so, energy that is needed for other activities. There is an optimal structure that takes all the activities of the bird into account. A bird which genetically knows best this optimum, will be selectively advantaged over the others (at least in respect to nest building).

Adaptations are optimums of lowest genetic cost. An adaptation represents a genetic knowledge of some past environment and need not necessarily be the best knowledge for the current environment. Generalists have greater adaptability than specialists, that is, they can "learn" more quickly about new environments.

3.10 Developmental Biology

The ideas of Waddington (1957, 1961) contributed significantly to the field of developmental biology. He considered how the development of organisms is affected by their environment. Development occurs along pathways (canals) which are controlled by the genes with selection (canalising) favouring the development of these pathways. If development is too strictly controlled the growing organism will not be very responsive to environmental changes. Waddington devised a model which he called an epigenetic landscape. Down this landscape flowed many canals that branched and interconnected. The developing organism takes certain pathways in its journey through this landscape. While it is travelling within a canal its development is fixed. Changes in the environment will not alter its direction. Here the sides of the canal are steep and buffer the development to follow a certain direction. Only extreme environmental conditions will cause a flow over the sides of this canal. However when the canal reaches a point where it divides into two,

the development of the organism is more sensitive to environmental changes and a course change is possible. Here the organism may develop one way or another depending on small environmental changes.

An organism may gain from developmental flexibility. It is advantaged by developing a form sympathetic to the environment in which it is growing rather than developing a fixed form, suitable to some average environment. Such characteristics as height, colour, weight, muscle development, and cunning will depend to varying extents on the environments encountered. In the development of muscle (say) an animal is advantaged by having that optimum amount of muscle needed for its niche. Too little muscle will not allow it to function properly, yet too much will be a genetic cost. A fixed genetic plan for a particular amount of muscle tissue would be disadvantageous in both times of plenty or scarcity. Muscle development is optimised by having genes whose expression is in part driven by environmental information.

In the development of the sex of some species of turtles, an environmental condition, sand temperature, has a significant impact on the developing embryo. This development can be seen here as the division of one development canal into two on the epigenetic landscape: one canal leads to the development of a male turtle, the other to a female. The point of division is where development can go either way and a small environmental variation is enough to do this. The turtle, while flexible on sex, cannot develop just a single front flipper (say). It will either form two or, if the environmental conditions are extreme, it will die. The development of the flippers is along a deep canal with steep walls that do not allow a change of canal.

Not all influences during development are beneficial. The human embryo is very sensitive to environmental changes and this sensitivity is reflected in the evolution of a constant environment for the embryo's

development; the womb. Drugs such as alcohol and diseases such as German measles can affect the embryonic development detrimentally. Drug addictions of the mother may pass through the placenta. In plants, severe defects result in the absence of certain trace elements. Such environmental factors are capable of redirecting canal flows.

Some authors consider the environment and genes of equal importance in the production of the phenotype. The genes are meaningless unless taken in the context of the environment in which they normally develop (Gray 1992). One environment results in a particular phenotype while another in a different phenotype. Selection is no longer on the gene but on the developmental system; the combined system of organism and environment. The internal (genetic) and external (environmental) components are intricately intertwined and cannot be separated.

A generalist's broad niche may be highly varied and so offspring may encounter different environments. It would be of advantage for an organism to develop alternative forms, forms that are suitable for the environments the adult is to live in. For example, an oak seed, falling on open ground grows into a broad thick-trunked tree with ample lower branches, while in a forest it has a tall slender trunk with no lower branches. Two different environments evoke two different structures. A generalist is selectively advantaged by having developmental flexibility through allowing early environmental variations to influence development. Only certain genetic knowledge is needed in certain environments yet a large store of knowledge will cater for many different environments. This has been called an "open program" or "phenotypic plasticity" - see Thompson 1991, Day, Pritchard and Schulter 1994, and Behera and Nanjundiah 1995.

If unity of the genetic knowledge and environmental influences is assumed, then selection must act on both genes and environment. It is

clear that selection acts on an organism, but it is not so clear how selection acts on environmental information. Griffiths and Gray argue that "evolution is best construed as differential replication of development processes" (1993:2). Developmental processes include such things as sunlight, rain and gravity. It is difficult to see how they reproduce. A plant needs sunlight for photosynthesis and its seeds will, as developing plants, also need light. Griffiths and Gray (1993) argue that persistent environmental features such as sunlight are part of the developmental system in the sense that the new plant would be subject to different selection pressures should the sunlight be of different strength. As well, by continuing to shine, the sun replicates that sunshine. However Gray and Griffiths go too far in taking environmental information as part of the replicating process (Sterelny, Smith and Dickson 1996).

I find a difficulty here. The differential replication of development processes will reflect the differential survival of organisms but not the differential survival of environmental information with which those organisms interact. While there is selection on environmental information there is no physical unit of environmental information that *survives* differentially. Sunlight always survives. It is true that environmental information, such as the atmosphere, may become highly altered through its coevolution with organisms. An oxygen molecule might survive differentially, depending on the activities of organisms. Here some physical processes may be inseparable from biological evolution. Selection may be on developmental processes in some circumstances.

Lastly, in any interaction of an organism and its environment, including development, it must be remembered that there is both directional and random selection pressures. In a study of *Drosophila* kept in constant environmental conditions, Lewontin (1978) found that "developmental

noise" in the development of the phenotype resulted in variations just as significant as those caused by genetic noise and environmental noise.

Organisms, particularly generalists, are selectively advantaged by genetic knowledge that codes for flexibility in development. From this the organism develops a phenotype suitable to the current environment rather than a phenotype suitable to some average environment. An organism is advantaged by genetic knowledge of a number of possible environments.

3.11 Complexity

The word "complexity" is reliant to a large extent on the human eye-view. A working machine may seem complex to one person yet simple to another. For an organism, complexity could be taken to mean the degree of intricacy of its structures and behaviours. It is obvious that a mammal is more complex than a single cell. Therefore, in some rough chronological order, life must increase in complexity. The first celled organisms had the least complexity; later developments had necessarily to be more complex. Yet single cells have not stopped evolving and have undergone an increase in internal complexity. The evolution of plants and animals both show, from fossil records, progressively more intricate organisms with greater complexity. There have been major steps within this development. The most significant was the development of sexual reproduction from asexual reproduction. This reproductive mechanism was one feature that could be considered as more complex than asexual reproduction. Other advances in complexity could be the evolution of eukaryote cells from prokaryotes, the evolution of the vertebrates and the development of the brain, and through this, language.

While there is a general increase in complexity through evolution, and it appears as an underlying feature of the evolutionary process, it is difficult to establish this as rule (McShea 1991, Grantham 1994).

Evolution is for survival, not an increase in complexity. At the same time, an increase in complexity usually accompanies evolution. It is possible that this increase may reflect the fact that the Earth is an evolving planet which has not yet achieved "organic maturity", and that, once this happens, decreases in complexity may be just as common as increases. This is probably part of the truth. The other part may be through the red queen effect (section 3.9). While a physical environment may be constant (sunlight density, soil fertility, rainfall and so on) competition between organisms may result in continual increase in complexity of adaptive features. A species must change at a certain rate just to match changes in other organisms. Any new adaptation requires more genetic knowledge and this knowledge will increase in organisms generally. Organisms improve their knowledge of other organisms.

The amount of genetic material within a cell has increased significantly over time (Stebbins and Ayala 1985:55). More complex organisms generally have more DNA per cell than simpler ones. There are a few exceptions, such as frogs, toads and newts, of which all have more DNA than humans (Dobzhansky 1970:17-18). Evolution could, in this light, be seen as a race by organisms to know their changing environments through greater complexity in genetic knowledge.

On the other hand, there are numerous cases where complexity decreases. For example, by moving underground moles appear to have undergone a decrease in complexity. Their eyes have degenerated and their life style seems simpler. This is to be expected as underground life would seem more specialised than the more varied life above ground. By moving underground the mole has become less of a generalist and more of a specialist. For this change to happen, it must have been selectively advantageous. The underground niche exerted less selection pressure than that above ground. If the below ground lifestyle is simpler, then, like the earlier example of insects adapting to cave life and forgoing

eyesight, the mole may have undergone selection pressures that led to a narrowing of its niche. It has undergone a loss of genetic knowledge.

Similarly, whales must have been selectively advantaged by returning to the sea. Possible advantages over the fishes may have been properties such as being warm blooded (which allows a higher metabolic rate and reduced sluggishness) or having the ability to breath air (survival is independent of the water oxygen levels). Whatever the case, their legs, in particular the bones, show degeneration to form fins. A watery environment appears a narrower niche in that it is more uniform than a terrestrial environment. On the other hand, certain structures of whales, such as the brain, may have increased in complexity. In one sense the whales may be less complex, in another, more complex.

Ecosystems are the next level up from species. Is there an increasing complexity in these? There is a general perception amongst ecologists that an increase in complexity relates to an increase in stability. Bookchin has observed that: "through differentiation, through variety, we achieve greater ecological stability ... The greater the variety of life forms that we have in our ecosystems the more stable they are likely to be" (1986:11). Yet a ecosystem where one or more species go to extinction is an ecosystem where a *loss* of species was necessary to obtain equilibrium. Here complexity (in terms of species numbers) has decreased. Ecosystems will become more or less complex depending on selection pressures within them. Like organisms, while many ecosystems may show increased stability through increased complexity, this cannot be established as a rule. Ecosystems will move in the direction of greatest stability and this may result in more or less complexity.

Hahlweg (1991) chooses a different argument for complexity. He argues that there is progress in evolution not through organisms becoming more complex, but by organisms, as dissipative structures in a

thermodynamic context (see section 3.18), becoming better able to maintain themselves far from thermodynamic equilibrium under increasingly heterogeneous environmental conditions. Organisms have become progressively better at converting energy (in the form of food eaten) into body structures. The chemical complexity (or efficiency) in metabolic management becomes successively more complex. This is almost a truism, as it is hard to imagine an animal being selectively more advantaged by having a less efficient thermodynamic system.

Evolution selects for genetic knowledge that allows an organism to better know its environment. If a generalist, through selection, becomes a specialist, its environment may be less varied. In this case, previous knowledge about aspects of an environment that is not necessary for survival will become a genetic cost to an organism and so be lost. To sum up roughly; organisms “move”, in terms of genetic knowledge, in the direction of least resistance. A move to a less varied environment will result in a loss of complexity (generalist to specialist) and a move to a more varied environment will involve an increase in complexity (specialist to generalist). As water flows down a gradient, the direction of evolution could also be considered as a movement along a gradient, a gradient defined by selection pressures, rather than the slope of the river bed . (As argued earlier this movement still requires particular genetic mutations that allow movement down this gradient.) I will use the term “move” here to mean a change in the genetic knowledge of an organism as it broadens or narrows its niche.

This generalisation is further open to modification. For example, the whale above may have lost complexity (in terms of genetic knowledge) in its move to the sea in a particular *ancestral* environment. At that time it may have been less complex than its land cousin. However, selection pressures operating on both since that time will have differentially changed their complexity such that the whale may be now more complex

than the modern equivalent of its land cousin. Different rates of evolution will reflect different rates of changes in complexity.

While animals may increase the complexity of their genetic knowledge, such an increase cannot be established as a rule. Generally, organisms move along a gradient, becoming more complex if the movement is to a broader niche, and less complex if it is to a narrower niche.

3.12 Coevolution and Teleology

Coevolution and teleology are inseparably linked. Coevolution generally means the evolution of two species whose niches overlap to the extent that each acts as a selection pressure on the other. Teleology in evolution, or the doctrine of adaptation to a definite purpose, suggests that evolution is "end directed". For example, the rabbit and fox are in a prey/predator relationship. The rabbit, as part of the fox's environment and so a directional selection pressure on the fox, "end directs" adaptations of that fox. Similarly, the fox "end directs" adaptations of the rabbit. Night feeding by rabbits will cause foxes to hunt at night. The development of large ears in rabbits for detection of small noises will select for stealthy foxes. Each is a selection pressure on the other. If the fox feeds only on the rabbit, and the rabbit has only the fox as a predator, they will become progressively more fine-tuned to each other's habits. If the fox has available to it a large variety of not very common species, it will need to become much more of a generalist, with a strategy that works for hunting each species. The rabbit too, if it is preyed upon by many species, will need a number of different strategies to evade them.

The fox and rabbit also live in a physical environment, and they will coevolve with this as well. Like saltwater or a desert, specific characteristics of an organism's environment will act as a selection pressure for particular characteristics in that organism. (As argued in 2.4,

an organism's form is a response to the environmental information it is exposed to). If a new niche with abundant food becomes available, species will move to fill it (assuming the necessary mutations occur). This appears teleological in the sense that the niche (an "end") seems to select for something to occupy it. Species moving to a niche evolve adaptations suitable for that niche. The niche moulds an organism to a particular form through the selection pressures it asserts. This can best be seen by the examples of parallel evolution given earlier. The similar physical conditions acting on the marsupials and the placentals produced a similar range of responses to environmental conditions. A saltwater environment produced eyes in fish and cephalopods yet selection operated on different archetypal structures. In both cases eyes achieved the same purpose, while their structural differences show their different beginnings.

If there are two competing species occupying the same niche, and the selection pressures are intense, and if the selection pressures of neighbouring niches are less, then the two competitors will diverge in form, resulting in a decrease of competition. This is similar to each species moving to vacant niches, or at least, niches where competition is reduced. The species move along a gradient from a high selection pressure to one of a low pressure. If competition in neighbouring niches is also intense this may result in narrowing the "band" or niche in which a species lives. Species will tend to become specialists in areas where the competition between the species is greatest (Laylor and Maynard Smith 1976). If competition is weak across a range of niches, or if competition is evenly spread, an organism may become a generalist, that is, occupy a broad niche.

Just as organisms change their genetic knowledge through selection pressures from environmental information, organisms can modify the environments in which they live. The most significant example of this is

the removal of carbon from the air by early anaerobic organisms allowing the oxygen concentration to increase and leading to the evolution of aerobic organisms. Here the changing atmosphere acted as a selection pressure, continually changing the form of the organisms that utilised it. This is similar to the red queen effect (section 3.9). An organism must evolve as fast as changes made to the atmosphere through the very same organisms. Here organisms must not only keep up (in terms of adaptations) with other organisms, but must keep up with a changing physical environment.

Organisms change their environments physically in numerous ways. The root systems of plants hold soil together, preventing erosion. This retention of soil by such plants as mangroves may cause silting of river beds and estuaries, leading to significantly new environments for animals to colonise. Root systems that bind soil particles together, allow the retention of more water and so an increase in evaporation through the plant's leaves. Some ninety percent of all the rainfall in the Amazon basin is circulated within it, never reaching the sea. Should vegetation cover be reduced, the volume of water circulation would be reduced proportionally. During the formation of new climates, organisms must evolve at a rate at least equal to the rate of their formation.

If environmental conditions are too severe a species may avoid certain parts of it. A niche is only that environment experienced by the organism. A bear that hibernates avoids the winter. The snow and ice that was a selection pressure on the ancestors of bears resulted in genetic knowledge that allows a hibernation during winter. There has been a reduction in the indeterminacy of the bear's environment. The bear now occupies a new niche, one that does not include snow and ice. Other organisms also narrow their niche. Various ground mammals have adopted feeding at night so as to reduce predation by foxes, hawks, and so on. It is conceivable that certain nocturnal animals do not "know"

sunlight, having never experienced it. Plants may respond to dry periods by becoming dormant or by restricting their form to seeds during the harsh period. Harsh environments of the plants are known genetically allowing the plant to modify its niche. Through coevolution, organisms developed a genetic knowledge of their habitats.

The term "coevolution" has also been used for less direct influences of one organism on another. Take mimicry as an example. Here a poisonous caterpillar, which advertises this fact with striking colours (say red stripes), will represent a selection pressure on other local caterpillars which are not poisonous. A colourless non poisonous caterpillar may occupy the same physical area yet utilise a different food and so not be in competition with the striped caterpillar. A variation in the bland caterpillar that looks a little like red stripes may give it a slight advantage due to the reluctance of a predator to risk poisoning. Over time this pressure may result in red stripes on the non poisonous caterpillar. Here one species is a selection pressure on another yet that second species has no effect on the first. The selection pressure that results in genetic change is unidirectional (Futuyma and Slatkin 1983).

A butterfly of South Africa derives nutrition from a red nectar-producing flower. An orchid has come to mimic this flower so as to be pollinated by the butterfly which mistakes it for the red nectar-producing flower (Johnson 1994). The flower is a selection pressure on the orchid, while the orchid exerts no pressure on the flower.

Organisms and their environments coevolve, each changing the other. A species must change at least as fast as the changes both of its competitors, and of its physical environment (the red queen effect). A species must "learn" (through genetic knowledge) how to modify its new environment.

3.13 Rate of Evolution

There has been much debate over the rate of evolution. The synthetic theory tells us that evolution results from the accumulation of many small variations. This concept has been challenged by Eldredge and Gould (1972, Gould and Eldredge 1977, Gould 1980). Briefly, their argument is as follows. Fossil records contain many gaps with these gaps the result of rapid evolutionary change leaving little fossil evidence. Between these rapid changes there are long periods where little morphological change in species occurs. Evolution is "punctuated" by bursts of species development followed by long periods of stability. They contend that the synthetic theory fails to account for these rapid changes. Microevolutionary processes are insufficient to explain macroevolutionary events; that is, the sudden appearance of new species. A revision is therefore needed of the current synthetic theory. In support of this belief it is assumed that palaeontologists are unable to find intermediate species to fill evolutionary gaps due to the formation of new species being so rapid that little evidence of the intermediate forms remain. Those supporting this view are often called "punctualists" while those who see the synthetic theory as sufficient to explain evolutionary phenomena are "gradualists".

The punctuated equilibrium theory has been widely criticised (Stebbins and Ayala 1981, 1985, Ridley 1980, Maynard Smith 1981a, Kellogg 1988, Sterelny 1992). The main criticism is that it is not clear what is and what is not rapid:

The dispute with the punctualists loses some of its focus when one recognises that it is partly an artifact of a radical difference in time scales: the time scale of the palaeontologists who propose the theory of punctuated equilibrium and that of the geneticists who were instrumental in formulating the

synthetic theory. Since successive layers in geologic strata may have been laid down tens of thousands of years apart, morphological changes that developed over thousands of generations may make an abrupt appearance in the fossil record. In contrast, geneticists refer to changes that require 200 generations or more as gradual, since they exceed the time span of all experiments except those on micro-organisms. In speaking on the one hand of sudden change and on the other of gradual evolution, the punctualists and the gradualists are in many cases talking about the same thing (Stebbins and Ayala 1985:60).

A second criticism is that morphological forms do not necessarily say anything about change. The work of palaeontologists involves the examination of fossils, however this is a record of morphological changes representing only the hard parts of animals. Large morphological changes leading to speciation may have occurred in the soft portions of animals, information not available to the palaeontologists. As Maynard Smith has pointed out: "there are on our beaches two species of periwinkle whose shells are indistinguishable, but which do not interbreed and of which one lays eggs and the other bears live young." (1993a:152). Here two morphologically similar animals are in fact quite different species. A palaeontologist examining a fossil record of these shells would see no difference.

It cannot be assumed that different parts of an organism evolve at the same rate. Much depends on the magnitude of selection pressures experienced. In the fossil record there is only a fragment of species traits. If the morphological evidence is not clear, then the claim of punctuated equilibrium needs to be justified. This explanation would need to show how stasis is maintained, why it breaks down, and how this achieved. (Sterelny 1992:42-43).

A third criticism is that the synthetic theory does not in fact imply that evolution should be gradual. If environmental conditions change rapidly, then organisms would experience changes in selection pressures that could lead to new species: "the intermediate forms are well adapted to neither their former niche nor to the one being colonised. So they will be neither long lasting nor widely distributed. So it is no surprise that these intermediaries are not found in the fossil record" (Sterelny 1992:44). The rate of evolution of a species may depend on such things as the mutation rate, the strength of selection pressures and the organism's generation length. New species have been created by human selection in *Drosophila* in a few generations by inducing a high mutation rate (Jones 1981). For generalists the rate of change of mutations, and the rate of evolution, may be under genetic control (see section 3.7). An organism may increase variation in its offspring as a response to varying environmental conditions.

The life style of an organism may also affect its rate of evolution. Specialist organisms that occupy a narrow niche would tend to speciate and so risk extinction more often than generalists which, through occupying a broad niche, have a greater genetic knowledge allowing a wider range of behaviours. They are more buffered against environmental variation. Elizabeth Vrba (from Lewin 1980) noted that of two groups of antelope, one, a specialist, had at least 27 species over the last six million years (from fossil evidence) while the other, a generalist, had only 3. The rate of speciation here is related to the habits of the animals, something not necessarily obvious from the morphological form.

The rate of evolution depends on selection pressures, the mutation rate, and the generation length. The synthetic theory is sufficient to account for any variation in these rates.

3.14 Level of Evolution and Group Evolution

Richard Dawkins (1976) has argued that selection is on the level of the gene rather than the individual. Here the genes compete with one another for survival; that is, for their retention within the gene pool. To demonstrate this he uses the example of a boat race. All rowers are needed to win the race, yet one poor rower is enough to lose it. This poor rower, a defective gene, will then be lost along with all the genes of the organism. For survival it is in the selfish interest of each rower to row as hard as he can so as to win and receive the reward (replication). Dawkins (1986) called the gene a replicator, and the body that carried the replicators, a vehicle.

Dawkins' model has come under fire. David Hull (1985:415) notes that certain paramecium, where a section of the cilia is removed and reversed, pass this characteristic on to offspring. Here the vehicle is also a replicator. Hull defines a replicator as "an entity that passes on its structure largely intact in successive replications" and an interactor as "an entity that interacts as a cohesive whole with its environment in such a way that this interaction *causes* replication to be differential" (1985:408). Hull also sees the gene, normally a replicator, as an interactor. In its replication it needs to unwind and so, during this process, it is subject to selection or change (mutation) by its environment. Hull chooses "interactor" over "vehicle" to cater for those simple organisms where the vehicle is of small size and so possibly indistinguishable from the replicator. If we consider the earlier example of replicating polynucleotides, here the replicator is indistinguishable from the interactor. The genotype *is* the phenotype. The interactor, or vehicle, becomes more distinct from the replicator as the extent of the phenotype increases. A distinct phenotype separates the genes from direct interaction with the environment.

Brandon (1985), Gould (1980) and Sober (1984), have argued that the interactor is the unit of selection rather than the gene. The interactor survives differentially, resulting in the differential survival of the replicator. Yet I see the two levels as intricately linked and beyond separation. The survival of an interactor directly affects the survival of all the genes associated with it. A selection on the interactor is also a selection on the replicator.

Mitchell (1987) suggests that selection involves two steps, interaction (through interactors or vehicles) and transmission (through replicators). Like Hull (1985) she questions whether the gene is not also an interactor. The unit of selection, then, can be either an interactor or a replicator. Kary (1988) argues against this, suggesting that while there may be two steps, it does not imply that the causal processes between them are different. Mitchell and Kary's use of "causal" arguments I believe to be unsatisfactory. As Maynard Smith points out (1978), both causal and functional explanations are necessary in biology. By "functional" he means a level of causal explanation that acts over the entire evolutionary history of the animal. The cause of a person's walking is the movement of his legs back and forth. However the functional reason that encompasses the entire evolutionary history of the human, is that the legs are used for movement in order to obtain food and to escape predators.

Following from this, it is all very well to debate the causal reasons for the interaction of genes and their environments, but one must also consider the reason as to why there are genes at all. Genes are knowledge about environments. If an organism has knowledge that allows it to build structure (the phenotype) as an aid to replication, then it will be selectively advantaged. The function of the phenotype is as a structural aid for the replication of the genes. Differential selection acts on the phenotype, which in turn differentially selects for genetic makeup. The

causal process is the same for each step, with that causal process being one of differential survival of variations.

I see little merit in the whole replicator/interactor/vehicle argument. It appears to be more an example of competing definitions, definitions for which there are always exceptions. Simple life forms, such as Hull's paramecium and replicating polynucleotides, are both interactors and replicators. With more complex, sexual organisms, it is not always clear what a replicator is. After meiotic division, only half the genes of each parent go to make up the next generation. Neither of the two parents replicate their genotypes completely. Recessive alleles may replicate but play no role in forming the phenotype. Some genes replicate yet appear, due to their enormous number of repetitions, not to play any role in the phenotype formation. A further difficulty is that during the process of replication, the genes may also be altered by mutation. These new genes could not be replicators or interactors.

Maynard Smith (1989, see also Shanahan 1990), recognised the problem with establishing just what exactly is a "unit of selection". He made a distinction between the "unit of selection" and the "unit of evolution". For something to be a unit of evolution, it must have properties of multiplication, heredity and variation (section 3.2). These three properties are necessary before evolution can take place. An organism is therefore a unit of evolution. Should any one of these properties be missing, evolution is not possible. An example used earlier was the cuckoo. Unless genetic knowledge exists that allows recognition, or partial recognition, of the egg or chick, then, while the cuckoo is a unit of selection, there is no unit of heredity (genes within the host bird) that this selection pressure can act on. Evolution cannot occur in respect to the host knowing about the cuckoo. To give another example, consider that some exotic disease invades a population and that there is no resistance to it. Because there is no genetic resistance, this disease is no different

from any other environmental information that randomly selects against an organism. The disease is a selection pressure on the phenotype, yet there is no unit of heredity such that a resistance to the disease can develop. Yet should there be new genetic knowledge (that comes through mutation) in some individual that reduces the severity of this disease, then the disease becomes a directional selection on the species. Through those animals with beneficial mutations, the species moves in the direction of least resistance. A genetic knowledge of the disease will invade the gene pool. The common cold has little genetic resistance (due to its rapid speciation) and so new forms spread quickly. It constitutes a unit of selection, yet there may not a unit of evolution in their host for selection to act on.

Another possible level of selection is that of the group. Whales that use air to encircle schools of fish and then swim up these columns of air swallowing the whole school, fishers netting schools of fish, insect swarms sprayed with deadly chemicals and so on, are all group selections. Selection on groups is commonplace. Yet as Maynard Smith argues: "there is no question that selection is acting on the groups. But it would be dangerous to think of the groups as units of evolution. If we did, we would expect the groups to evolve adaptations ensuring their survival" (1989:122). The fish and insects undergo group selection, yet these groups cannot evolve as there is no unit of group evolution. The unit of heredity is the gene. Group selection then, can only lead to the differential survival of genes, the phenotype of which is the individual. Group selection can only lead to individual evolution.

Are there some cases where group selection leads to group evolution? Multicelled organisms probably evolved from single celled organisms that clustered to act as a mutualistic whole. But clustering is not enough for group evolution. The unit of heredity must be a single one (a germ cell). If all the cells of a cluster can reproduce separately, we are back to

the individual being the unit of evolution. Group evolution only occurs where the interest of every cell is to contribute to replication of the whole group. If a cluster has a single cell to reproduce the cluster, then this cell is a unit of evolution at the level of the group. For a multicelled organism the interest of all the cells in the germ cell is guaranteed if they are genetically identical. Through supporting the germ cell they reproduce themselves. There is group evolution. The situation is different for a group of distinct cells. Here each cell has the opportunity, by adopting new structures or behaviours, to become more numerous than other cells, and so internal competition can occur.

The functioning of a colony of termites seems to parallel the functioning of a cluster of cells that makes up a multicelled organism. In termites, differential development in the young is effected through nutritional signals so as to cause different forms from the queen to arise, such as workers and soldiers. The different forms are still genetically identical to the queen. The colony could be considered as a cluster of cells whose cells are free ranging. It is not a case of numerous different organisms. A mutation in the genes of a worker termite does not affect heredity, just as a mutation in a cell of a multicelled organism does not affect heredity. Only mutations within germ cells, in this case the queen or drone, will lead to genetic change. Selection of termite colonies is group selection in the same sense that group selection acts on a multicelled organism. The unit of evolution for the termite and the multicelled organism is the germ cell.

All cells of a multicelled organism must also cooperate in order to survive. The human body has specialised cells (grouped as organs) to perform certain functions. It also has free moving cells that race around the body killing intruders (phagocytes). The body's cells perform in different ways because the genetic knowledge within them is differentially repressed. Selection is clearly on the ability of the group to

function as a whole, not just on the level of the individual. As single cells or organs cannot reproduce themselves, they cannot enter into competition with each other. All these different cells, however, have the same genetic content and so a contribution to the survival of the germ cell is a contribution to their own reproduction (considered in detail in 3.16). Occasionally cells do gain the ability for individual reproduction (cancers) and, as can be expected, these cells immediately compete with the body's other cells.

Under varying environments, some species are polymorphic showing different behaviours *for different environments*. For example, conditions of food shortages and high densities cause locusts to swarm and so behave as a social unit rather than individuals (Barrass 1974). This must have some selective advantage to occur. Here group behaviour is driven by genetic knowledge and the swarm is really a multitude of individuals co-operating for mutual benefit. A beneficial genetic change in any one still reflects individual evolution rather than group evolution. While there is group selection (say through aerial spraying) there is not group evolution. The swarming is a mutualistic relationship which helps the survival of individuals, similar to the grouping of many mammals and fish. There is no unit of evolution at the level of the group and so swarming does not represent group evolution.

The smallest group could be considered a group of genes contained within a cell. This is selected as a whole through the differential survival of the cell they are located in. Selection on the cell could be seen as group evolution. For the cell to survive, all genes must cooperate as in Dawkins' boat race (considered above). As with the multicelled organisms, if the genes within the cell could individually reproduce then selection on the cell would not always result in group evolution.

Selection can occur on many levels yet evolution can only occur for units of heredity that are capable of variation and differential survival. As genes are the only heredity units, evolution can only occur at this level.

3.15 Game Theory

A game is an interaction between an organism and its environment. Organisms act in ways that they believe (genetically) are selectively advantageous. An organism will act in that particular way it perceives to be best for it. This may not be the best action, yet the organism does not know this. It does not have a perfect genetic knowledge of its environment. Its environment is in part indeterminate from its eye-view. Yet it does the best it can according to its knowledge. Every organism has a phylogenetic knowledge of past environments. It is with this knowledge that the organism interacts with its *current* environment; known through information collected by its senses. An interaction is continually assessed by the organism with new interactions undertaken if necessary. An amoeba encountering an impassable object tries another direction. The benefit of any interaction could be called a “payoff”. The payoff can be negative if the interaction is detrimental. Some animals initiate better actions than others and these will be selectively advantaged. In this sense, the life of any organism can be considered as a series of interactions or games.

That component of an interaction initiated by an organism could be called a “strategy”. These strategies result from genetic knowledge and the organism is subject to various directional and random selections. Strategies that return positive payoffs will selectively advantage the organism having them, increasing its chances of survival. This does not mean they are the best strategies possible, but they are strategies that are better than or at least as good as other strategies held by competitors. There may well be better strategies but these must first appear as genetic

variations and then be retained through selection. Strategies do not represent an exact understanding of an environment, but represent an optimum less than the exact value. For example, the wing represents a strategy of a bird that allows flight. Yet no wing is perfectly adapted to flight. Such an adaptation would require a greater investment, one not justified in terms of survival.

The conflict between two competing coevolving animals represents a particular type of interaction. Maynard Smith (1982b) called such an interaction a Hawk/Dove game. By "Hawk" is meant a strategy that is aggressive and by "Dove" a strategy where an organism retreats from aggression.

Consider the following game given by Maynard Smith and Price (1973). The participating animals have weapons capable of serious injury and three actions are possible. In a conflict an animal may use conventional tactics (C), dangerous tactics (D), or it may retreat (R). While an animal may use its dangerous weapons in capturing prey or in fights with animals incapable of retaliation it rarely uses these tactics with conspecifics. For example, a lion will kill prey by gripping the throat and causing suffocation. This method would not work with another lion as the attacking lion would be open to severe injuries such as being disembowelled by the kicking legs of the lion held. Of course, the strategy for the prey is always to retreat, but for another lion, seeking mating rights say, a limited conflict is the usual outcome. The study allowed five strategies, made from various combinations of the three possible actions tactics. By constraining the model to a finite number of strategies, it can be modelled mathematically. The five strategies are:

- (1) 'Mouse'. Never plays D. If receives D, retreats at once before there is any possibility of receiving a serious injury.

Otherwise plays C until the contest has lasted a preassigned number of moves.

(2) 'Hawk'. Always plays D. Continues the contest until he is seriously injured or his opponent retreats.

(3) 'Bully'. Plays D if making the first move. Plays D in response to C. Plays C in response to D. Retreats if opponent plays D a second time.

(4) 'Retaliator'. Plays C if making the first move. If opponent plays C, plays C, (but plays R if contest has lasted a preassigned number of moves). If opponent plays D, with a high probability retaliates by playing D.

(5) 'Prober-Retaliator'. If making the first move, or after opponent has played C, with a high probability plays C and with a low probability plays D (but plays R if contest has lasted a preassigned number of moves). After giving a probe, reverts to C if opponent retaliates, but "takes advantage" by continuing to play D if opponent plays C. After receiving a probe, with high probability plays D (Maynard Smith and Price 1973:16).

After many simulated contests, the Retaliator strategy was found to give the highest payoff. This strategy is an evolutionary stable strategy (ESS). Such a strategy is one where, if an organism plays any other strategy or combination of strategies, it will receive a lower payoff than an organism that consistently plays the Retaliator strategy. Organisms playing other strategies will be selectively disadvantaged and so such strategies will be lost through the loss of the genes that drive such alternative strategies. Behaviours of organisms will, over time, be reduced in variety to behaviours that are ESSs. The genetic knowledge of the species (in respect to this particular contest) is constant and any new ideas (new strategies) fail.

The ESS cannot be invaded by a strategy consisting of some other combination of C, D or R. Yet it can be invaded by new tactics. Say an organism modifies D (dangerous tactics) by biting the other animal. D has now changed to a new value and this will result in a new ESS evolving. Another possibility is that while the strategies stay the same, a perturbation of the environment may result in these strategies returning different payoffs than previously. In the contest above, the Prober-Retaliator was very close to being an ESS. A small change in environmental conditions may result in this having a greater payoff than Retaliator and so the genetic knowledge of an organism will change to make this the prominent strategy (behaviour) used.

The idea of an ESS is widely applicable. For example, consider the ratio of sexes in elephant seals. About two percent of elephant seals father all of the next generation. Why then are ninety eight percent of the young not born female and two percent male? Surely this would maximise population growth? Certainly the population would grow more rapidly, but evolution is not about survival of the species; it is about survival of the individual. The species is not a unit of evolution. Say a beach has a population of two males and ninety eight females. Then a mother that produced a male would on average pass her genes, through this male, to about thirty pups ($100/3$). Had she produced a female, her genes would pass to only one pup in the next generation. The number of male seals produced would therefore increase, through genetic knowledge favouring the birth of males. In contrast, say there are a majority of males. A female having a male pup would, on average, pass her genes through her son to less than one seal. The mother would be advantaged by producing a female, thereby guaranteeing at least one pup. A population with too many males or too many females produces a situation more favourable to the opposite sex. Therefore a sex ratio of 1:1 is the best strategy. All other ratios of males to females attempted will

produce, on average, a lower payoff. A ratio of 1:1 is an ESS and it is seals that adopt this strategy that will be selectively advantaged.

An organism adopts strategies (driven by genetic knowledge) in its interactions with its environment that maximise its payoff. Strategies that produce the highest payoff (ESS), become fixed in the population. The ESS is an optimum of lowest genetic cost.

3.16 Genetic Altruism

For true altruism (or altruism in a strong sense), an organism would have to behave in such a way as to diminish its own chances of reproduction while promoting the chances of other organisms (Trivers 1985). An organism's interaction with another organism has to be a net cost to the organism.

The helping of kin (kin selection - see Hamilton 1964, Taylor and Frank 1996) is often referred to as altruism. In a study of ground squirrels Sherman (1982) considered alarm calls given to warn other squirrels of perceived danger. To overcome difficulties in identifying which squirrel was giving a call, and to whom, the animals were individually marked. The observations collected over a three year period led to the conclusion that calls were made to assist relatives. But altruistic behaviour to kin members is not true altruism; rather it is behaviour to increase the level of inclusive fitness (section 3.4). Many acts that at first sight seem altruistic are actually instances of kin selection.

In northern Australia there is a toad (*Bufo marinus*) that has poisonous glands on the back of the head resulting in death to the animal that eats it. It might appear that this can be of no benefit to the eaten toad and so his death is an altruistic one, in that it helps all toads. However, if the toad has already reproduced then his offspring will gain some protection

from the removal of the predator. Self sacrifice in order to protect offspring is a form of kin selection. This is usually seen in cases where the parents have few offspring (often in mammals) and so a high genetic investment in offspring. Genetically, the survival of the offspring may be as important, or nearly as important, as that of the parent. The parent(s) may place themselves at considerable risk in order to protect their offspring.

Like assistance to kin, mutualism and reciprocal altruism are often considered as altruism (DeNault and McFarlane 1995). Yet two organisms, in assisting each other, both receive a benefit from that help. A bee that fertilises a flower gets a reward of nectar. Both flower and bee receive a net benefit from this interaction. Many cases of apparent altruism are really cases of either kin selection or symbiosis. Neither of these cases are of interest in this section. I will consider only interactions that result in a net cost to an organism; altruism in the strong sense.

Such an interaction has been claimed for slime moulds (DeAngelo *et al.* 1990, Hilson *et al.* 1994):

In a state of starvation, originally independent slime mold amoebae aggregate to form a multicellular "slug" and attempt to crawl to an area more conducive to dispersal of their spores. When such an area is found, cells differentiate into stalk cells and spore capsule cells, which jointly form fruiting bodies suited for dispersal of spores to new areas. The amoebae which become the stalk cells sacrifice themselves in order to allow the amoebae that give rise to the spores in the spore capsule to disperse and survive. The more amoeboid cells that sacrifice themselves in the stalk, the taller the fruiting body becomes. This increased height allows the cells in the spore capsule a greater opportunity to be dispersed via

increased exposure to wind or passing animals (Hilson *et al.* 1994:4).

It appears that the cells that sacrifice themselves to become stalk cells are acting altruistically. They give themselves no chance of reproduction, rather they enhance the chances of others. Yet the experiments showed (by statistical analysis of the ratio between the spore capsule diameter and the stalk length) that, in a pure culture of amoebae (that is, the amoebae are genetically related) there was a higher probability of amoebae cells willing to sacrifice themselves to form the stalk than in a slug resulting from two different strains. If cells are more likely to sacrifice themselves for genetically related individuals, then this is a case of kin selection. Like the termites, the worker sacrifices itself to the queen because the queen is genetically identical and so through the queen reproducing, the worker reproduces.

The much larger spore capsules and shorter stalks of the mixed cultures are used as evidence of decreased altruism. Fewer amoebas were willing to sacrifice themselves. Thus an organism is less likely to sacrifice itself for an unrelated individual. It is not clear though, that any cell that goes to make up a stalk is actually sacrificing itself. For instance, what is the *mechanism* by which an amoeba chooses to become a stalk or a spore cell? Our poor knowledge of cell chemistry may prevent us from understanding this mechanism. For the "choice" to exist each cell must have within it genetic knowledge that caters for both behaviours, remaining as a stalk or migrating to the top of the stalk as a capsule. A cell that "chooses" to become a stalk cell would on average produce less offspring and so would become in proportion less numerous in the population, eventually disappearing.

It is possible to imagine different explanations. For example, say the first cells to reach the top release some chemicals that inhibit others from

getting any further. Here every cell struggles its utmost to get to the top, achieving this feat differentially. If this is the case, what is apparent altruism becomes a simple struggle for survival. The longer stalks for the pure cultures could result from a reduced inhibiting chemical production in respect to kin.

It seems far from clear, then, that strong altruism is established here. An argument against altruism in slime moulds is made by Tullock (1990). He calls the slug a "society of nuclei":

The individual nuclei need have no Hamiltonian nepotism for other nuclei. It is simply that their own survival is only possible within this kind of society. If they mutate in such a way as to give themselves an advantage they make the whole society less viable. Thus, they select themselves out - as well, of course, as selecting out a very large number of other nuclei which do not carry that particular mutation. Presumably such mutations have occurred in the past and have left no descendants (1990:155).

Tullock's argument is essentially the same as Dawkins' uses in his boat race analogy. I will assume that the nuclei, like the genes within a cell, contain different knowledge. All nuclei must row together to benefit as a whole. Here the society is like a single cell that survives or fails depending on the genes within it. But there is a problem here. When a cell reproduces *all* the genes are reproduced. When a society of nuclei reproduce only some of the nuclei reproduce (those in the capsule). As argued earlier (3.12), for a group to undergo group evolution there must be units of heredity at the group level. This is true for the cell in that the genes are a unit of heredity. But for a society of nuclei the unit of reproduction is a nuclei. There is no unit of heredity at the group level. Tullock's argument therefore fails. It is more likely that the slime

mould's behaviour is like the swarm of locusts. Each locust and mold is an individual in its own right with unique genetic knowledge. The moulds form a stalk and capsule under adverse conditions because it is a response that increases *individual* fitness. Like the locust swarm where individuals seek food, the strong will get more than the weak. There is a struggle by nuclei to be part of the capsule but not all achieve this.

The opposite of altruism, spitefulness, is also seen in a few species. FitzGerald (1992:201) argues: "female threespine sticklebacks show spiteful behaviour. In the field, they seek out conspecifics' eggs to attack while largely ignoring those of a closely related sympatric species, the blackspotted stickleback. This occurs despite the fact that the latter's nests are more abundant and less well protected". The idea of spiteful here is that an animal will harm itself in order to harm other conspecifics, which are competitors, even more. This is similar to altruism in that in both cases there is a net loss to the initiator of the act. It takes energy to harm conspecifics. However for the recipient of spite there is a greater loss. These types of behaviour are related to cannibalism. "Cannibalism is not an aberrant behaviour limited to confined or highly stressed populations, but is normal response to many environmental factors. ... Cannibalism is an intraspecific predator-prey interaction that may also function as a means of interference competition, limiting population size before the resource itself becomes limiting" (Fox 1975:102). It would be selectively advantageous to kill competitors. This is most easily done when they are young and defenceless. Even better is to eat the competitors killed thereby deriving nutrition as well. Spiteful behaviour is a successful strategy for some organisms.

The examples above indicate that altruism, in the strong sense, will not directly evolve as altruistic acts will be selectively disadvantageous. If altruism is to occur it must occur only because it is a *by-product* of the normal selection processes that underlie evolutionary theory. To show

this would seem to be a difficult task. Two things are needed. Firstly, it would be necessary to see whether an organism can intentionally choose *any* action that is not beneficial to itself. Secondly, it is necessary to show that at least one of these actions benefits another organism. I will attempt to do this.

Konrad Lorenz (1952), in a study of water shrews, found that these small carnivorous animals memorised their surroundings during their pre-adult development. They often gave prominence to this mental image when moving around rather than relying on information received from their senses about their environment. A shrew that encountered a stone along a path will incorporate this into its mental pattern of its environment, regularly jumping the stone in its movements. Later, if the stone is removed, the shrew will still jump in that same place. Now the jumping of a non-existent stone is an action that is a cost to an individual in terms of wasted energy. Yet this cost could be justified in evolutionary terms. It may require less resources to form an early mental image of an environment that allows more rapid movement than to calculate afresh new paths of movement, even given the occasional mistake. Genetic habits formed by organisms, while selectively advantageous in a general sense, may not be advantageous in particular cases. Yet the genetic cost of having increased mental powers may be greater than producing the occasional inefficiency when interacting with the environment. Here a detrimental behaviour can be selectively advantageous from an evolutionary view point, when considering long term behaviour. Overall, the habit is beneficial.

Now, consider that a shrew eats a number of red striped water bugs. Say the next water bug of the same appearance eaten is very bad tasting. From this the shrew decides not to eat any more bugs with red stripes. Also say the first bugs eaten were mimics of the later bad tasting type. The shrew is now aware of there being two different tasting bugs, yet, as

it cannot distinguish them, leaves both alone. Here a habit has been formed that is selectively advantageous in a general sense, but not advantageous in a particular sense. The habit could be called a *general strategy*. The shrew that has the opportunity to eat a mimic, and declines to do so, is acting *altruistically* from the eye-view of the mimic yet selfishly from its own eye-view. Yet this selfish behaviour is clearly selectively advantageous to the shrew. An organism may evolve habits that, while a cost in a particular case, are of overall benefit. It is a cost to the shrew not to eat an edible water bug but overall it is better not to eat any, as the eating of an occasional bad tasting bug is worse than the eating of many good bugs. Organisms, while they can only adopt selfish strategies, will occasionally take actions that are altruistic from the eye-view of other organisms. (This is clearly separate from symbiosis as help is not intentionally given, nor is it reciprocated.)

There is a second possibility of altruism that is different from the above. There is a lag period between the formation of genetic knowledge and its use. An organism has certain genetic knowledge that was a response to environments experienced by its ancestors, yet this knowledge may not be an optimum for the current environment. If it is not optimum then it is likely that there are ongoing selection pressures on the organism to update that knowledge (once again change is possible only given the necessary mutations). A species, if undergoing genetic change, indicates by this process that its knowledge of past environments is not that most selectively advantageous for the current environment. For example, host birds whose nests are targets of cuckoos, respond to a beckoning mouth as a prompt for chick feeding. Yet should the host be able to distinguish the beckoning mouths, it could defeat the parasite. The inability of some hosts to produce new knowledge so as to expel cuckoo's eggs and chicks, results in their continual exploitation. While the host bird only acts selfishly, its inefficiency in these selfish acts, that is its genetic ignorance for certain environments, amounts to the host performing an act that is

altruistic in the eye-view of the cuckoo. Organisms can be exploited if their genetic knowledge is for past environments not current environments. Acts driven by ancestral genes can be exploited so that they are a cost to the organism in their current environments, that is, altruistic in the eye-view of the exploiting organism. An organism, while its knowledge may be appropriate to some past environments, may have gaps in this knowledge in respect to the current environment. While the organism only acts selfishly, some acts may be altruistic in the eye-view of other organisms.

Imagine a predator such as a lion. It will stalk its prey using energy and time to do so. Even so it will only be successful occasionally. The prey resist it. They have a genetic knowledge of it. If a hunting lion approached an animal that just stood there and allowed itself to be killed, this would be most unusual. It would only happen in real life if the animal had no genetic knowledge of the danger of lions. From the lion's eye-view the animal would be acting altruistically. It has provided it a free meal with no energy cost to the lion. The killing of the dodo in Mauritius is an example of this. The bird was genetically ignorant of the danger of humans. Its genetic knowledge allowed it survival in terms of a past environment, but not a current one (the presence of humans). Genetic ignorance may result in selfish behaviours that are altruistic from the eye-views of other animals.

Here are two possible ways that an organism may take actions in its current environment that are of cost to itself. Should these actions be beneficial to another organism, then this would be altruism in the strong sense, that is, an organism performs an action that is of cost to itself and of benefit to another. To a third party observing such actions, it would appear that they are altruistic actions. Yet the actions are only altruistic in the eye-view of the recipient and selfish from the eye-view of the organism initiating the action.

Altruism may result from a selfish action. Such an action is initiated by genetic knowledge that is for a general strategy (a genetic habit), or from genetic knowledge that is from ignorance of the current environment. While the organism initiating the action only acts selfishly, the action may be at cost to the organism and of benefit to the recipient of the action.

3.17 Thermodynamics

The second law of thermodynamics states that the entropy (the amount of disorder) can only increase or stay constant in a closed system over a given time period. Entropy theory plays a crucial part in evolution theory (Collier 1986). The growth of plants and animals represents an increase in order and so a decrease in entropy. The Earth however is not a closed system and it is the energy throughput of low entropy structures, photons, that allows the construction of more ordered systems, while at the same time allowing for an increase in entropy. To explain this, consider the sunlight that falls on leaves and other parts of the environment. Sunlight falling on leaves is converted to chemical energy with a little increase in entropy. Sunlight not falling on leaves becomes heat, a large increase in entropy that results in the warming of the planet. The sunlight that falls on leaves is now energy that is available to the plant and can be used to make structure. It is also available to animals that eat the plant.

Through the activities of animals and the decay of plant structure, eventually all the sunlight that falls on the leaf will be converted to heat. Of two equal units of sunlight, the one falling on the leaf will take a longer path in its conversion to heat than the light on the soil. This path allows, through the conversion of energy to heat, work to be done.

The thermodynamic approach adds a new dimension to our knowledge of evolution. Consider two organisms, one of which can produce structure from sunlight more efficiently than the other. The more efficient organism will be selectively advantaged. By being a more efficient organism, for the same amount of energy it can produce more structure; it has a higher metabolic efficiency. A thermodynamicist would be justified in seeing evolution in terms of a plant's ability to manage the energy from the original sunlight. Such a belief would not diminish evolution theory but enrich it, adding a new metabolic selection pressure to the environmental selection pressures that already act to optimise structural form and behaviours used. "The fact that natural selection may be conceived as differential survival of informed pathways of energy flow does not undermine the core ... of the Darwinian tradition" (Weber *et al.* 1989:376).

The idea of thermodynamic pathways provide an exciting new perspective upon evolution. They allow a thermodynamic approach to ecological problems. For example, Johnson argues:

In general, it may be said that the removal of a dominant predator will tend to increase biomass whereas removal of dominant vegetation will reduce biomass. Removal of a predator eliminates one energy transformation stage. Because each energy transformation has a very high energy demand, biomass can increase even though total energy input remains constant. This implies that the specific energy flux (the energy to support unit biomass) will decline as biomass increases because of longer retention time within the system of each unit of energy assimilated (1992:39).

This justifies the pyramidal structure of organism development, with predators such as humans and eagles on the top, in terms of energy flows and entropy increase. A common thermodynamic argument today is that the western nations should reduce their consumption of meat. Such a practice would remove, in part, one energy stage and so make possible a greater biomass of humans for the same energy throughput. It is likely that these thermodynamic arguments will, in time, become a significant part of evolution theory.

An organism experiences selection pressures for metabolic efficiency. This efficiency is part of an organism's genetic knowledge. The more efficient synthesis of a certain structure will allow the energy saved to be used elsewhere, or alternatively, less food to be consumed.

3.18 Summary

The first life on Earth consisted of replicating chemicals. These had the properties of multiplication, variation and heredity. The chemicals, and the organisms that followed, evolved from a dead environment; that is, some variations of chemicals were selectively advantaged over others and so had more chance of survival. The units of heredity of an organism (the genes) are a record of directional and random selection pressures that existed in ancestral environments. Through this genetic knowledge an organism reduced the indeterminacy of its environments. This knowledge is not exact but represents an optimum understanding, one that is genetically most cost efficient. Organisms can be divided roughly into two groups; generalists with broad niches; and specialists with narrow niches. An organism's knowledge increases or decreases depending on a gradient, the slope of which is related to the selection pressures experienced. Generalists that become specialists move along a gradient reducing their genetic knowledge in the process. Specialists must increase their knowledge to become generalists.

An organism and its environment coevolve, each changing the other. The organism is advantaged if it can modify its environment. It evolves genetic knowledge to allow it to do this. Generalists, more so than specialists, are selectively advantaged in letting environmental factors play a role in the formation of structures and behaviours. This allows the development of a phenotype more suitable to the current environment rather than to some average environment. The evolution of the senses, and the processing of the information collected by them, increases an organism's ability to function in its current environment and so enhances its survival.

An organism adopts strategies in its interactions with its environment that it perceives (genetically) as maximising its payoff. Strategies that produce higher payoffs than others (ESSs), become fixed in a population. The strategies chosen are those that provide for the selfish interests of the organism. This may include mutualistic relationships or reciprocal altruism. These interactions are entirely selfish. Some genetic altruism (in the eye-view of the recipient) occurs which is the indirect outcome of evolution. A general selfish strategy may, for efficiency, require altruism in particular cases. Altruism may also result from genetic ignorance of the current environment.

The ideas above apply to genetic knowledge and I have assumed that the organisms used as examples have not engaged in any cultural exchanges of knowledge. It is this cultural knowledge that is the subject of the next chapter. Are the underlying processes responsible for genetic knowledge different from cultural knowledge? I will argue that, while there are considerable differences between the two, these differences are only manifestations of the two different environments in which these knowledge processes take place (a physical and a mental environment)

and that the fundamental processes underlying both are identical; that is, an entity has variation and this variation survives differentially.