

## CHAPTER 1 – WHY ARE PEOPLE?

If superior creatures from space ever visit earth, the first question they will ask, in order to assess the level of our civilization, is: 'Have they discovered evolution yet?' (1)

The argument of this book is that we, and all other animals, are machines created by our genes. (2)

Much as we might wish to believe otherwise, universal love and the welfare of the species as a whole are concepts that simply do not make evolutionary sense. (2)

... it is a fallacy [...] to suppose that genetically inherited traits are by definition fixed and unmodifiable. (3)

Blackheaded gulls nest in large colonies, the nests being only a few feet apart. When the chicks first hatch out they are small and defenseless and easy to swallow. It is quite common for a gull to wait until a neighbour's back is turned, perhaps while it is away fishing, and then pounce on one of the neighbour's chicks and swallow it whole. It thereby obtains a good nutritious meal, without having to go to the trouble of catching a fish, and without having to leave its own nest unprotected. (5)

Mantises are large carnivorous insects. They normally eat smaller insects such as flies, but they will attack almost anything that moves. When they mate, the male cautiously creeps up on the female, mounts her, and copulates. If the female gets the chance, she will eat him, beginning by biting his head off, either as the male is approaching, or immediately after he mounts, or after they separate. It might seem most sensible for her to wait until copulation is over before she starts to eat him. But the loss of the head does not seem to throw the rest of the male's body off its sexual stride. Indeed, since the insect head is the seat of some inhibitory nerve centres, it is possible that the female improves the male's sexual performance by eating his head. If so, this is an added benefit. The primary one is that she obtains a good meal. (5)

Perhaps we can sympathize more directly with the reported cowardly behaviour of emperor penguins in the Antarctic. They have been seen standing on the brink of the water, hesitating before diving in, because of the danger of being eaten by seals. If only one of them would dive in, the rest would know whether there was a seal there or not. Naturally nobody wants to be the guinea pig, so they wait, and sometimes even try to push each other in. (5)

... many ground-nesting birds perform a so-called 'distraction display' when a predator such as a fox approaches. The parent bird limps away from the nest, holding out one wing as though it were broken. The predator, sensing easy prey, is lured away from the nest containing the chicks. Finally the parent bird gives up its pretence and leaps into the air just in time to escape the fox's jaws. It has probably saved the life of its nestlings, but at some risk to itself. (6)

... group selection theory now commands little support within the ranks of those professional biologists who understand evolution, it does have great intuitive appeal. Successive generations of zoology students are surprised, when they come up from school, to find that it is not the orthodox point of view. For this they are hardly to be blamed, for in the *Nuffield Biology Teachers' Guide*, written for advanced level biology schoolteachers in Britain, we find the following: 'In higher

animals, behaviour may take the form of individual suicide to ensure the survival of the species,' The anonymous author of this guide is blissfully ignorant of the fact that he has said something controversial. In this respect he is in Nobel Prize-winning company. Konrad Lorenz, in *On Aggression*, speaks of the 'species preserving' functions of aggressive behaviour, one of these functions being to make sure that only the fittest individuals are allowed to breed. This is a gem of a circular argument, but the point I am making here is that the group selection idea is so deeply ingrained that Lorenz, like the author of the *Nuffield Guide*, evidently did not realize that his statements contravened orthodox Darwinian theory [individual selection]. (8)

Perhaps one reason for the great appeal of the group-selection theory is that it is thoroughly in tune with the moral and political ideals that most of us share. We may frequently behave selfishly as individuals, but in our more idealistic moments we honour and admire those who put the welfare of others first. We get a bit muddled over how widely we want to interpret the word 'others', though. Often altruism within a group goes with selfishness between groups. This is a basis of trade unionism. At another level the nation is a major beneficiary of our altruistic self-sacrifice, and young men are expected to die as individuals for the greater glory of their country as a whole. Moreover, they are encouraged to kill other individuals about whom nothing is known except that they belong to a different nation. (Curiously, peace-time appeals for individuals to make some small sacrifice in the rate at which they increase their standard of living seems to be less effective than war-time appeals for individuals to lay down their lives.) (9)

The feeling that members of one's own species deserve special moral consideration as compared with members of other species is old and deep. Killing people outside war is the most seriously-regarded crime ordinarily committed. The only thing more strongly forbidden by our culture is eating people (even if they are already dead). We enjoy eating members of other species, however, many of us shrink from judicial execution of even the most horrible<sup>3</sup> human criminals, while we cheerfully countenance the shooting without trial of fairly mild animal pests. Indeed we kill members of other harmless species as a means of recreation and amusement. A human foetus, with no more human feeling than an amoeba, enjoys a reverence and legal protection far in excess of those granted to an adult chimpanzee. Yet the chimp feels and thinks and – according to recent experimental evidence – may even be capable of learning a form of human language. The foetus belongs to our own species, and is instantly accorded special privileges and rights because of it. Whether the ethic of 'speciesism', to use Richard Ryder's term, can be put on a logical footing any more sound than that of 'racism', I do not know. What I do know is that it has no proper basis in evolutionary biology. (10)

... I must argue for my belief that the best way to look at evolution is in terms of selection occurring at the lowest level of all. In this belief I am heavily influenced by G. C. Williams's great book *Adaptation and Natural Selection*. The central idea I shall make use of was foreshadowed by A. Weismann in pre-gene days at the turn of the century – his doctrine of the 'continuity of the germ-plasm'. I shall argue that the fundamental unit of selection, and therefore of self-interest, is not the species, nor the group, nor even, strictly, the individual. It is the gene, the unit of heredity. (11)

## CHAPTER 2 – THE REPLICATORS

Darwin's theory of evolution by natural selection is satisfying because it shows us a way in which simplicity could change into complexity, how unordered atoms could group themselves into every more complex patterns until they end up manufacturing people. (12)

... before the coming of life on earth, some rudimentary evolution of molecules could have occurred by ordinary processes of physics and chemistry. There is no need to think of design or purpose or

directedness. If a group of atoms in the presence of energy falls into a stable pattern it will tend to stay that way. The earliest form of natural selection was simply a selection of stable forms and a rejection of unstable ones. There is no mystery about this. It had to happen by definition. (13)

We do not know what chemical raw materials were abundant on earth before the coming of life, but among the plausible possibilities are water, carbon dioxide, methane, and ammonia: all simple compounds known to be present on at least some of the other planets in our solar system. Chemists have tried to imitate the chemical conditions on the young earth. They have put these simple substances in a flask and supplied a source of energy such as ultraviolet light or electric sparks – artificial simulation of primordial lightning. After a few weeks of this, something interesting is usually found inside the flask: a weak brown soup containing a large number of molecules more complex than the ones originally put in. In particular, amino acids have been found – the building blocks of proteins, one of the two great classes of biological molecules. Before these experiments were done, naturally-occurring amino acids would have been thought of as diagnostic of the presence of life. If they had been detected on, say Mars, life on that planet would have seemed a near certainty. Now, however, their existence need imply only the presence of a few simple gases in the atmosphere and some volcanoes, sunlight, or thundery weather. More recently, laboratory simulations of the chemical conditions of earth before the coming of life have yielded organic substances called purines and pyrimidines. These are building blocks of the genetic molecule, DNA itself.

Processes analogous to these must have given rise to the 'primeval soup' which biologists and chemists believe constituted the seas some three to four thousand million years ago. The organic substances became locally concentrated, perhaps in drying scum round the shores, or in tiny suspended droplets. Under the further influence of energy such as ultraviolet light from the sun, they combined into larger molecules. Nowadays large organic molecules would not last long enough to be noticed: they would be quickly absorbed and broken down by bacteria or other living creatures. But bacteria and the rest of us are late-comers, and in those days large organic molecules could drift unmolested through the thickening broth.

At some point a particularly remarkable molecule was formed by accident. We will call it the *Replicator*. It may not necessarily have been the biggest or the most complex molecule around, but it had the extraordinary property of being able to create copies of itself. This may seem a very unlikely sort of accident to happen. So it was. It was exceedingly improbable. In the lifetime of a man, things that are that improbable can be treated for practical purposes as impossible. That is why you will never win a big prize on the football pools. But in our human estimates of what is probable and what is not, we are not used to dealing in hundreds of millions of years. If you filled in pools coupons every week for a hundred million years you would very likely win several jackpots.

Actually a molecule that makes copies of itself is not as difficult to imagine as it seems at first, and it only had to arise once. Think of the replicator as a mould or template. Imagine it as a large molecule consisting of a complex chain of various sorts of building block molecules. The small building blocks were abundantly available in the soup surrounding the replicator. Now suppose that each building block has an affinity for its own kind. Then whenever a building block from out in the soup lands up next to a part of the replicator for which it has an affinity, it will tend to stick there. The building blocks that attach themselves in this way will automatically be arranged in a sequence that mimics that of the replicator itself. It is easy then to think of them joining up to form a stable chain just as in the formation of the original replicator. This process could continue as a progressive stacking up, layer upon layer. This is how crystals are formed. On the other hand, the two chains might split apart, in which case we have two replicators, each of which can go on to make further copies.

A more complex possibility is that each building block has affinity not for its own kind, but reciprocally for one particular other kind. Then the replicator would act as a template not for an identical copy, but for a kind of 'negative', which would in its turn re-make an exact copy of the original positive. For our purposes it does not matter whether the original replication process was

positive-negative or positive-positive, though it is worth remarking that the modern equivalents of the first replicator, the DNA molecules, use positive-negative replication. What does matter is that suddenly a new kind 'stability' came into the world. Previously it is probable that no particular kind of complex molecule was very abundant in the soup, because each was dependent on building blocks happening to fall by luck into a particular stable configuration. As soon as the replicator was born it must have spread its copies rapidly throughout the seas, until the smaller building block molecules became a scarce resource, and other larger molecules were formed more and more rarely.

So we seem to arrive at a large population of identical replicas. But now we must mention an important property of any copying process: it is not perfect. Mistakes will happen. I hope there are no misprints in this book, but if you look carefully you may find one or two. They will probably not seriously distort the meaning of the sentences, because they will be 'first generations' errors. But imagine the days before printing, when books such as the Gospels were copied by hand. All scribes, however careful, are bound to make a few errors, and some are not above a little wilful 'improvements'. If they all copied from a single master original, meaning would not be greatly perverted. But let copies be made from other copies, which in their turn were made from other copies, and errors will start to become cumulative and serious. We tend to regard erratic copying as a bad thing, and in the case of human documents it is hard to think of examples where errors can be described as improvements. I suppose the scholars of the Septuagint could at least be said to have started something big when they mistranslated the Hebrew word for 'young woman' into the Greek word for 'virgin', coming up with the prophecy: 'Behold a virgin shall conceive and bear a son ...' Anyway, as we shall see, erratic copying in biological replicators can in a real sense give rise to improvement, and it was essential for the progressive evolution of life that some errors were made. We do not know how accurately the original replicator molecules made their copies. Their modern descendants, the DNA molecules, are astonishingly faithful compared with the most high-fidelity human copying process, but even they occasionally make mistakes, and it is ultimately these mistakes that make evolution possible. Probably the original replicators were far more erratic, but in any case we may be sure that mistakes were made, and these mistakes were cumulative.

As mis-copying were made and propagated, the primeval soup became filled by a population not of identical replicas, but of several varieties of replicating molecules, all 'descended' from the same ancestor. Would some varieties have been more numerous than others? Almost certainly yes. Some varieties would have been inherently more stable than others. Certain molecules, once formed, would be less likely than others to break up again. These types would become relatively numerous in the soup, not only as a direct logical consequences of their 'longevity', but also because they would have a long time available for making copies of themselves. Replicators of high longevity would therefore tend to become more numerous and, other things being equal, there would have been an 'evolutionary trend' towards greater longevity in the population of molecules.

But other things were probably not equal, and another property of a replicator variety that must have had even more importance in spreading it through the population was speed of replication or 'fecundity'. If replicator molecules of type *A* make copies of themselves on average once a week while those of type *B* make copies of themselves once an hour, it is not difficult to see that pretty soon type *A* molecules are going to be far outnumbered, even if they 'live' much longer than *B* molecules. There would therefore probably have been an 'evolutionary trend' towards higher 'fecundity' of molecules in the soup. A third characteristic of replicator molecules which would have been positively selected is accuracy of replication. If molecules of type *X* and type *Y* last the same length of time and replicate at the same rate, but *X* makes a mistake on average every tenth replication while *Y* makes a mistake only every hundredth replication, *Y* will obviously become more numerous. The *X* contingent in the population loses not only the errant 'children' themselves, but also their descendants, actual or potential. (14-17)

To return to the primeval soup, it must have become populated by stable varieties of molecule; stable in that either the individual molecules lasted a long time, or they replicated rapidly, or they replicated accurately. Evolutionary trends toward these three kinds of stability took place in the following sense: if you had sampled the soup at two different times, the later sample would have contained a higher proportion of varieties with high longevity / fecundity / copying-fidelity. This is essentially what a biologist means by evolution when he is speaking of living creatures, and the mechanism is the same – natural selection.

Should we then call the original replicator molecules 'living'? Who cares? I might say to you 'Darwin was the greatest man who has ever lived', and you might say 'No, Newton was', but I hope we would not prolong the argument. The point is that no conclusion of substance would be effected whichever way our argument was resolved. The fact of the lives and achievements of Newton and Darwin remain totally unchanged whether we label them 'great' or not. Similarly, the story of the replicator molecules probably happened something like that way I am telling it, regardless of whether we choose to call them 'living'. Human suffering has been caused because too many of us cannot grasp that words are only tools for our use, and that the mere presence in the dictionary of a word like 'living' does not mean it necessarily has to refer to something definite in the real world. Whether we call the early replicators living or not, they were the ancestors of life; they were our founding fathers.

The next important link in the argument, one that Darwin himself laid stress on (although he was talking about animals and plants, not molecules) is *competition*. The primeval soup was not capable of supporting an infinite number of replicator molecules. For one thing, the earth's size is finite, but other limiting factors must also have been important. In our picture of the replicator acting as a template our mould, we supposed it to be bathed in a soup rich in the small building block molecules necessary to make copies. But when the replicators became numerous, building blocks must have been used up at such rate that they became a scarce and precious resource. Different varieties or strains of replicator must have competed for them. We have considered the factors that would have increased the numbers of favoured kinds of replicator. We can now see that less-favoured varieties must actually have become *less* numerous because of competition, and ultimately many of their lines must have gone extinct. There was a struggle for existence among replicator varieties. They did not know they were struggling, or worry about it; the struggle was conducted without any hard feelings, indeed without feelings of any kind. But they were struggling, in the sense that any mis-copying that resulted in a new higher level of stability, or a new way of reducing the stability of rivals, was automatically preserved and multiplied. The process of improvement was cumulative. Ways of increasing stability and of decreasing rivals' stability became more elaborate and more efficient. Some of them may even have 'discovered' how to break up molecules of rival varieties chemically, and to use the building blocks so released for making their own copies. These proto-carnivores simultaneously obtained food and removed competing rivals. Other replicators perhaps discovered how to protect themselves, either chemically, or by building a physical wall of protein around themselves. This may have been how the first living cells appeared. Replicators began not merely to exist, but to construct for themselves containers, vehicles for their continued existence. The replicators that survived were the ones that built *survival machines* for themselves to live in. The first survival machines probably consisted of nothing more than a protective coat. But making a living got steadily harder as new rivals arose with better and more effective survival machines. Survival machines got bigger and more elaborate and the process was cumulative and progressive.

Was there to be any end of the gradual improvement in the techniques and artifices used by the replicators to ensure their own continuation in the world? There would be plenty of time for improvement. What weird engines of self-preservation would the millennia bring forth? Four thousand million years on, what was to be the fate of the ancient replicators? They did not die out, for they are past masters of the survival arts. But do not look for them floating loose in the sea; they gave up that cavalier freedom long ago. Now they swarm in huge colonies, safe inside gigantic lumbering robots, sealed off from the outside world, communicating with it by tortuous indirect routes, manipulating it by remote control. They are in you and in me; they created us,

body and mind; and their preservation is the ultimate rationale for our existence. They have come a long way, those replicators. Now they go by the name of genes, and we are their survival machines. (18-20)

### CHAPTER 3 – IMMORTAL COILS

We are survival machines, but 'we' does not mean just people. It embraces all animals, plants, bacteria, and viruses. (21)

Different sorts of survival machine appear very varied on the outside and in their internal organs. An octopus is nothing like a mouse, and both are quite different from an oak tree. Yet in their fundamental chemistry they are rather uniform, and, in particular, the replicators that they bear, the genes, are basically the same kind of molecule in all of us – from bacteria to elephants. We are all survival machines for the same kind of replicator – molecules called DNA – but there are many different ways of making a living in the world, and the replicators have built a vast range of machines to exploit them. (21)

DNA works in mysterious ways. (21)

A. G. Cairns-Smith has made the intriguing suggestion that our ancestors, the first replicators, may have been not organic molecules at all, but inorganic crystals – minerals, little bits of clay. (21-22)

A DNA molecule is a long chain of building blocks, small molecules called nucleotides. Just as protein molecules are chains of amino acids, so DNA molecules are chains of nucleotides. A DNA molecule is too small to be seen, but its exact shape has been ingeniously worked out by indirect means. It consists of a pair of nucleotide chains twisted together in an elegant spiral; the 'double helix'; the 'immortal coil'. The nucleotide building blocks come in only four different kinds, whose names may be shortened to *A*, *T*, *C*, and *G*. These are the same in all animals and plants. A *G* building block from a man is identical in every particular to a *G* building block from a snail. But the *sequence* of building blocks in a man is not only different from that in a snail. It is also different – though less so – from the sequence in every other man (except in the special case of identical twins). (22)

DNA molecules do two important things. Firstly they replicate, that is to say they make copies of themselves. This has gone on non-stop ever since the beginning of life, and the DNA molecules are now very good at it indeed. As an adult, you consist of a thousand million million cells, but when you were first conceived you were just a single cell, endowed with one master copy of the architect's plans. This cell divided into two, and each of the two cells received its own copy of the plans. Successive divisions took the number of cells up to 4, 8, 16, 32, and so on into the billions. At every division the DNA plans were faithfully copied, with scarcely any mistakes.

It is one thing to speak of the duplication of DNA. But if the DNA is really a set of plans for building a body, how are the plans put into practice? How are they translated into the fabric of the body? This brings me to the second important thing DNA does. It indirectly supervises the manufacture of a different kind of molecule – protein. The haemoglobin which was mentioned in the last chapter is just one example of the enormous range of protein molecules. The coded message of the DNA, written in the four-letter nucleotide alphabet, is translated in a simple mechanical way into another alphabet. This is the alphabet of amino acids which spells out protein molecules.

Making proteins may seem a far cry from making a body, but it is the first small step in that direction. Proteins not only constitute much of the physical fabric of the body; they also exert sensitive control over all the chemical processes inside the cell, selectively turning them on and off at precise times and in precise places. Exactly how this eventually leads to the development of a

baby is a story which it will take decades, perhaps centuries, for embryologists to work out. But it is a fact that it does. Genes do indirectly control the manufacture of bodies, and the influence is strictly one way: acquired characteristics are not inherited. No matter how much knowledge and wisdom you acquire during your life, not one jot will be passed on to your children by genetic means. Each new generation starts from scratch. A body is the genes' way of preserving the genes unaltered. (23)

I said that the plans for building a human body are spelt out in 46 volumes. In fact this was an over-simplification. The truth is rather bizarre. The 46 chromosomes consist of 23 *pairs* of chromosomes. We might say that, filed away in the nucleus of every cell, are two alternative sets of 23 volumes of plans. Call them Volume 1a and Volume 1b, Volume 2a and Volume 2b etc., down to Volume 23a and Volume 23b. Of course the identifying numbers I use for volumes and, later, pages, are purely arbitrary.

We receive each chromosome intact from one of our two parents, in whose testis or ovary it was assembled. Volumes 1a, 2a, 3a, ... came, say, from the father. Volumes 1b, 2b, 3b, ... came from the mother. It is very difficult in practice, but in theory you could look with a microscope at the 46 chromosomes in any one of your cells, and pick out the 23 that came from your father and 23 that came from your mother.

The paired chromosomes do not spend all their lives physically in contact with each other, or even near each other. In what sense then are they 'paired'? In the sense that each volume coming originally from the father can be regarded, page for page, as a direct alternative to one particular volume coming originally from the mother. For instance, Page 6 of Volume 13a and Page 6 of volume 13b might both be 'about' eye colour; perhaps one says 'blue' while the other says 'brown'. (25)

The gene for brown eyes is dominant to the gene for blue eyes. A person has blue eyes only if both copies of the relevant page are unanimous in recommending blue eyes. (26)

I have described the normal division of a cell into two new cells, each one receiving a complete copy of all 46 chromosomes. This normal cell division is called *mitosis*. But there is another of cell division called *meiosis*. This occurs only in the production of the sex cells; the sperms or eggs. Sperms and eggs are unique among our cells in that, instead of containing 46 chromosomes, they contain only 23. this is, of course, exactly half of 46 – convenient when they fuse in sexual fertilization to make a new individual! Meiosis is a special kind of cell division, taking place only in testicles and ovaries, in which a cell with the full double set of 46 chromosomes divides to form sex cells with the single set of 23 (all the time using the human numbers for illustration).

A sperm, with its 23 chromosomes, is made by the meiotic division of one of the ordinary 46-chromosome cells in the testicles. Which 23 are put into any given sperm cell? It is clearly important that a sperm should not get just any old 23 chromosomes: it mustn't end up with two copies of Volume 13 and none of Volume 17. It would theoretically be possible for an individual to endow one of his sperms with chromosomes which came, say, entirely from his mother; that is Volume 1b, 2b, 3b, ... 23b. In this unlikely event, a child conceived by the sperm would inherit half her genes from her paternal grandmother, and none from her paternal grandfather. But in fact this kind of gross, whole-chromosome distribution does not happen. The truth is rather more complex. Remember that the volumes (chromosomes) are to be thought of as loose-leaf binders. What happens is that, during the manufacture of the sperm, single pages, or rather multi-page chunks, are detached and swapped with the corresponding chunks from the alternative volume. So, one particular sperm cell might make up its Volume 1 by taking the first 65 pages from Volume 1a and pages 66 to the end from Volume 1b. This sperm cell's other 22 volumes would be made up in a similar way. Therefore every sperm cell made by an individual is unique, even though all his sperms assembled their 23 chromosomes from bits of the same set of 46 chromosomes. Eggs are made in a similar way in ovaries, and they too are all unique. (26-27)

A gene is defined as any portion of chromosomal material that potentially lasts for enough generations to serve as a unit of natural selection. (28)

The average life-expectancy of a genetic unit can conveniently be expressed in generations, which can in turn be translated into years. If we take a whole chromosome as our presumptive genetic unit, its life story lasts for only one generation. Suppose it is your chromosome number 8a, inherited from your father. It was created inside one of your father's testicles, shortly before you were conceived. It had never existed before in the whole history of the world. It was created by the meiotic shuffling process, forged by the coming together of pieces of chromosome from your paternal grandmother and your paternal grandfather. It was placed inside one particular sperm, and it was unique. The sperm was one of several millions, a vast armada of tiny vessels, and together they sailed into your mother. This particular sperm (unless you are a non-identical twin) was the only one of the flotilla which found harbour in one of your mother's eggs – that is why you exist. The genetic unit we are considering, your chromosome number 8a, set about replicating itself along with all the rest of your genetic material. Now it exists, in duplicate form, all over your body. But when you in your turn come to have children, this chromosome will be destroyed when you manufacture eggs (or sperms). Bits of it will be interchanged with bits of your maternal chromosome number 8b. In any one sex cell, a new chromosome number 8 will be created, perhaps 'beter' than the old one, perhaps 'worse', but, barring a rather improbable coincidence, definitely different, definitely unique. The life-span of a chromosome is one generation. (29-30)

What I am doing is emphasizing the potential near-immortality of a gene, in the form of copies, as its defining property. To define a gene as a single cistron is good for some purposes, but for the purposes of evolutionary theory it needs to be enlarged. The extent of the enlargement is determined by the purpose of the definition. We want to find the practical unit of natural selection. To do this we begin by identifying the properties that a successful unit of natural selection must have. In the terms of the last chapter, these are longevity, fecundity, and copying-fidelity. We then simply define a 'gene' as the largest entity which, at least potentially, has these properties. The gene is a long-lived replicator, existing in the form of many duplicate copies. It is not infinitely long-lived. Even a diamond is not literally everlasting, and even a cistron can be cut in two by crossing-over. The gene is defined as a piece of chromosome which is sufficiently short for it to last, potentially, for *long enough* for it to function as a significant unit of natural selection.

Exactly how long is 'long enough'? There is no hard and fast answer. It will depend on how severe the natural selection 'pressure' is. That is, on how much more likely a 'bad' genetic unit is to die than its 'good' allele. This is a matter of quantitative detail which will vary from example to example. The largest practical unit of natural selection – the gene – will usually be found to lie somewhere on the scale between cistron and chromosome. (35-36)

However independent and free genes may be in their journey through the generations, they are very much *not* free and independent agents in their control of embryonic development. They collaborate and interact in inextricably complex ways, both with each other, and with their external environment. (36-37)

The question of why we die of old age is a complex one, and the details are beyond the scope of this book. In addition to particular reason, some more general ones have been proposed. For example, one theory is that senility represents an accumulation of deleterious copying errors and other kinds of gene damage which occur during the individual's lifetime. Another theory, due to sir Peter Medawar, is a good example of evolutionary thinking in terms of gene selection. Medawar first dismisses traditional arguments such as: 'Old individuals die as an act of altruism to the rest of the species, because if they stayed around when they were too decrepit to reproduce, they would clutter up the world to no good purpose.' As Medawar points out, this is a circular argument, assuming what it sets out to prove, namely that old animals are too decrepit to

reproduce. It is also a naïve group-selection or species-selection kind of explanation, although that part of it could be rephrased more respectably. Medawar's own theory has a beautiful logic. [...] late-acting lethal [gene] will be more stable in the gene pool than an early-acting lethal [gene]. A gene that is lethal in an older body may still be successful in the gene pool, provided its lethal effect does not show itself until after the body has had time to do at least some reproducing. [...] According to this theory then, senile decay is simply a by-product of the accumulation in the gene pool of late-acting lethal and semi-lethal genes, which have been allowed to slip through the net of natural selection simply because they are late-acting. The aspect that Medawar himself emphasizes is that selection will favour genes that have the effect of postponing the operation of other, lethal genes, and it will also favour genes that have the effect of hastening the effect of good genes. It may be that a great deal of evolution consists of genetically-controlled changes in the time of onset of gene activity. (40-41)

Female greenflies can bear live, fatherless, female offspring, each one containing all the genes of its mother. (Incidentally, an embryo in her mother's 'womb' may have an even smaller embryo inside her own womb. So a greenfly female may give birth to a daughter and a grand-daughter simultaneously, both of them being equivalent to her own identical twins). (43)

#### CHAPTER 4 – THE GENE MACHINE

Survival machines began as passive receptacles for the genes, providing little more than walls to protect them from the chemical warfare of their rivals and the ravages of accidental molecular bombardment. In the early days they 'fed' on organic molecules freely available in the soup. This easy life came to an end when the organic food in the soup, which had been slowly built up under the energetic influence of centuries of sunlight, was all used up. A major branch of survival machines, now called plants, started to use sunlight directly themselves to build up complex molecules from simple ones, re-enacting at much higher speed the synthetic processes of the original soup. Another branch, now known as animals, 'discovered' how to exploit the chemical labours of the plants, either by eating them, or by eating other animals. Both main branches of survival machines evolved more and more ingenious tricks to increase their efficiency in their various ways of life, and new ways of life were continually being opened up. Sub-branches and sub-sub-branches evolved, each one excelling in a particular specialized way of making a living: in the sea, on the ground, in the air, underground, up trees, inside other living bodies. This sub-branching has given rise to the immense diversity of animals and plants which so impresses us today.

Both animals and plants evolved into many-celled bodies, complete copies of all the genes being distributed to every cell. We do not know when, why, or how many times independently, this happened. Some people use the metaphor of a colony, describing a body as a colony of cells. I prefer to think of the body as a colony of *genes*, of the cell as a convenient working unit for the chemical industries of genes. (46)

... Roger Payne has pointed out that the acoustics of the sea have certain peculiar properties, which mean that the exceeding loud 'song' of some whales could theoretically be heard all the way round the world, provided the whales swim at a certain depth. [...] The speed of sound in water is such that it would take nearly two hours for the song to travel across the Atlantic Ocean and for a reply to return. I suggest this as an explanation for the fact that some whales deliver a continuous soliloquy, without repeating themselves, for a full eight minutes. They then go back to the beginning of the song and repeat it all over again, many times over, each complete cycle lasting about eight minutes. (53-54)

Genes work by controlling protein synthesis. This is a powerful way of manipulating the world, but it is slow. It takes months of patiently pulling protein strings to build an embryo. The whole point

about behaviour, on the other hand, is that it is fast. It works on a time-scale not of months but of seconds and fractions of seconds. Something happens in the world, an owl flashes overhead, a rustle in the long grass betrays prey, and in milliseconds nervous systems crackle into action, muscles leap, and someone's life is saved – or lost. Genes don't have reaction-times like that. [...] the genes can only do their best *in advance* by building a fast executive computer for themselves, and programming it in advance with rules and 'advice' to cope with as many eventualities as they can 'anticipate'. But life [...] offers too many different possible eventualities for all of them to be anticipated. [...] the genes have to 'instruct' their survival machines not in specifics, but in the general strategies and tricks of the living trade. (55)

One way for genes to solve the problem of making predictions in a rather unpredictable environment is to build in a capacity for learning. Here the program may take the form of the following instructions to the survival machine: 'Here is a list of things defined as rewarding; sweet taste in the mouth, orgasm, mild temperature, smiling child. And here is a list of nasty things: various sorts of pain, nausea, empty stomach, screaming child. If you should happen to do something that is followed by one of the nasty things, don't do it again, but on the other hand repeat anything that is followed by one of the nice things.' The advantage of this sort of programming is that it greatly cuts down the number of detailed rules that have to be built into the original program; and it is also capable of coping with changes in the environment that could not have been predicted in detail. On the other hand, certain predictions have to be made still. In our example the genes are predicting that sweet taste in the mouth, and orgasm, are going to be 'good' in the sense that eating sugar and copulating are likely to be beneficial to gene survival. The possibility of saccharine and masturbation are not anticipated according to this example; nor are the dangers of over-eating sugar in our environment where it exists in unnatural plenty. (57)

What about simulation? Well, when you yourself have a difficult decision to make involving unknown quantities in the future, you do go in for a form of simulation. You *imagine* what would happen if you did each of the alternatives open to you. You set up a model in your head, not of everything in the world, but of the restricted set of entities which you think may be relevant. You may see them vividly in your mind's eye, or you may see and manipulate stylized abstractions of them. In either case it is unlikely that somewhere laid out in your brain is an actual spatial model of the events you are imagining. But [...] the details of how your brain represents its model of the world are less important than the fact that it is able to use it to predict possible events. Survival machines that can simulate the future are one jump ahead of survival machines who can only learn on the basis of overt trial and error. The trouble with overt trial is that it takes time and energy. The trouble with overt error is that it is often fatal. Simulation is both safer and faster.

The evolution of the capacity to simulate seems to have culminated in subjective consciousness. Why this should have happened is, to me, the most profound mystery facing modern biology. There is no reason to suppose that electronic computers are conscious when they simulate, although we have to admit that in the future they may become so. Perhaps consciousness arises when the brain's simulation of the world becomes so complete that it must include a model of itself. Obviously the limbs and body of a survival machine must constitute an important part of its simulated world; presumably for the same kind of reason, the simulation itself could be regarded as part of the world to be simulated. Another word for this might indeed be 'self-awareness', but I don't find this a fully satisfying explanation of the evolution of consciousness, and this is only partly because it involves an infinite regress – if there is a model of the model, why not a model of the model of the model ... ? (59)

I am trying to build up the idea that animal behaviour, altruistic or selfish, is under the control of genes in only an indirect, but still very powerful, sense. By dictating the way survival machines and their nervous systems are built, genes exert ultimate power over behaviour. But the moment-to-moment decisions about what to do next are taken by the nervous system. Genes are the primary policy-makers; brains are the executives. But as brains became more highly developed, they took

over more and more of the actual policy decisions, using tricks like learning and simulation in doing so. The logical conclusion to this trend, not yet reached in any species, would be for the genes to give the survival machines a single overall policy instruction: do whatever you think best to keep us alive. (60)

Honey bees suffer from an infectious disease called foul brood. This attacks the grubs in their cells. Of the domestic breeds used by beekeepers, some are more at risk from foul brood than others, and it turns out that the difference between strains is, at least in some cases, a behavioural one. There are so-called hygienic strains which quickly stamp out epidemics by locating infected grubs, pulling them from their cells and throwing them out of the hive. The susceptible strains are susceptible because they do not practise this hygienic infanticide. The behaviour actually involved in hygiene is quite complicated. The workers have to locate the cells of each diseased grub, remove the wax cap from the cell, pull out the larva, drag it through the door of the hive, and throw it on the rubbish tip. (60)

Some survival machines exploit the sexual desires of others. Bee orchids induce bees to copulate with their flowers, because of their strong resemblance to female bees. What the orchid has to gain from this deception is pollination, for a bee who is fooled by two orchids will incidentally carry pollen from one to the other. Fireflies (which are really beetles) attract their mates by flashing lights at them. Each species has its own particular dot-dash flashing pattern, which prevents confusion between species, and consequent harmful hybridization. Just as sailors look out for the flash patterns of particular lighthouses, so fireflies seek the coded flash patterns of their own species. Female of the genus *Photuris* have 'discovered' that they can lure males of the genus *Photinus* if they imitate the flashing code of a *Photinus* female. This they do, and when a *Photinus* male is fooled by the lie into approaching, he is summarily eaten by the *Photuris* female. Sirens and Lorelei spring to mind as analogies, but Cornishmen will prefer to think of the wreckers of the old days, who used lanterns to lure ships on to the rocks, and then plundered the cargoes that spilled out of the wrecks. (65)

## CHAPTER 5 – AGGRESSION: STABILITY AND THE SELFISH MACHINE

To a survival machine, another survival machine (which is not its own child or another close relative) is part of its environment, like a rock or a river or a lump of food. It is something that gets in the way, or something that can be exploited. It differs from a rock or a river in one important respect: it is inclined to hit back. This is because it too is a machine that holds its immortal genes in trust for the future, and it too will stop at nothing to preserve them. Natural selection favours genes that control their survival machines in such a way that they make the best use of their environment. This includes making the best use of other survival machines, both of the same and of different species. (66)

Survival machines of the same species tend to impinge on each others' lives more directly. This is for many reasons. One is that half the population of one's own species may be potential mates, and potentially hard-working and exploitable parents to one's children. Another reason is that members of the same species, being very similar to each other, being machines for preserving genes in the same kind of place, with the same kind of way of life, are particularly direct competitors for all the resources necessary for life. To a blackbird, a mole may be a competitor, but it is not nearly so important a competitor as another blackbird. Moles and blackbirds may compete for worms, but blackbirds and blackbirds compete with each other for worms *and* for everything else. If they are members of the same sex, they may also compete for mating partners. For reasons that we shall see, it is usually the males who compete with each other for females. This means that a male might benefit his own genes if he does something detrimental to another male with whom he is competing.

The logical policy for a survival machine might therefore seem to be to murder its rivals, and then, preferably, to eat them. Although murder and cannibalism do occur in nature, they are not as common as a naïve interpretation of the selfish gene theory might predict. Indeed Konrad Lorenz, in *On Aggression*, stresses the restrained and gentlemanly nature of animal fighting. For him the notable thing about animal fights is that they are formal tournaments, played according to rules like those of boxing or fencing. Animals fight with gloved fists and blunted foils. Threat and bluff take the place of deadly earnest. Gestures of surrender are recognized by victors, who then refrain from dealing the killing blow or bite that our naïve theory might predict. (67)

Why is it that animals do not go all out to kill rival members of their species at every possible opportunity?

The general answer to this is that there are costs as well as benefits resulting from outright pugnacity, and not only the obvious costs in time and energy. For instance, suppose that *B* and *C* are both my rivals, and I happen to meet *B*. It might seem sensible for me as a selfish individual to try to kill him. But wait. *C* is also my rival, and *C* is also *B*'s rival. By killing *B*, I am potentially doing a good turn to *C* by removing one of his rivals. I might have done better to let *B* live, because he might then have competed or fought with *C*, thereby benefiting me indirectly. The moral of this simple hypothetical example is that there is no obvious merit in indiscriminately trying to kill rivals. In a large and complex system of rivalries, removing one rival from the scene does not necessarily do any good: other rivals may be more likely to benefit from his death than oneself. This is the kind of hard lesson that has been learned by pest-control officers. You have a serious agricultural pest, you discover a good way to exterminate it and you gleefully do so, only to find that another pest benefits from the extermination even more than human agriculture does, and you end up worse off than you were before.

On the other hand, it might seem a good plan to kill, or at least fight with, certain particular rivals in a discriminating way. If *B* is an elephant seal in possession of a large harem full of females, and if I, another elephant seal, can acquire his harem by killing him, I might be well advised to attempt to do so. But there are costs and risks even in selectivity pugnacity. It is to *B*'s advantage to fight back, to defend his valuable property. If I start a fight, I am just as likely to end up dead as he is. Perhaps even more so. He holds a valuable resource, that is why I want to fight him. But why does he hold it? Perhaps he won it in combat. He has probably beaten off other challengers before me. He is probably a good fighter. Even if I win the fight and gain the harem, I may be so badly mauled in the process that I cannot enjoy the benefits. Also, fighting uses up time and energy. These might be better conserved for the time being. If I concentrate on feeding and on keeping out of trouble for a time, I shall grow bigger and stronger. I'll fight him for the harem in the end, but I may have a better chance of winning eventually if I wait, rather than rush in now. (68)

The essential concept Maynard Smith introduces [based on a branch of mathematics known as Game Theory] is that of the *evolutionarily stable strategy*, an idea that he traces back to W. D. Hamilton and R. H. MacArthur. A 'strategy' is a pre-programmed behavioural policy. An example of a strategy is: 'Attack opponent; if he flees pursue him; if he retaliates run away.' It is important to realize that we are not thinking of the strategy as being consciously worked out by the individual. Remember that we are picturing the animal as a robot survival machine with a pre-programmed computer controlling the muscles. [...] An evolutionarily stable strategy or ESS is defined as a strategy which, if most members of a population adopt it, cannot be bettered by an alternative strategy. (69)

An ESS is stable, not because it is particularly good for the individuals participating in it, but simply because it is immune to treachery from within. (72)

Members of one's own species are made of meat too. Why is cannibalism relatively rare? [...] adults do sometimes eat the young of their own species. Yet adult carnivores are never to be

seen actively pursuing other adults of their own species with a view to eating them. Why not? We are still so used to thinking in terms of the 'good of the species' view of evolution that we often forget to ask perfectly reasonable questions like: 'Why don't lions hunt other lions?' Another good question of a type which is seldom asked is: 'Why do antelopes run away from lions instead of hitting back?'

The reason lions do not hunt lions is that it would not be an ESS for them to do so. A cannibal strategy would be unstable [...]. there is too much danger of retaliation. This is less likely to be true in contests between members of different species, which is why so many prey animals run away instead of retaliating. It probably stems originally from the fact that in an interaction between two animals of different species there is a built-in asymmetry which is greater than that between members of the same species. Whenever there is strong asymmetry in a contest, ESSs are likely to be conditional strategies dependent on the asymmetry. Strategies analogous to 'if smaller, run away; if larger, attack' are very likely to evolve in contests between members of different species because there are so many available asymmetries. Lions and antelopes have reached a kind of stability by evolutionary divergence, which has accentuated the original asymmetry of the contest in an ever-increasing fashion. They have become highly proficient in the arts of, respectively, chasing, and running away. A mutant antelope that adopted a 'stand and fight' strategy against lions would be less successful than rival antelopes disappearing over the horizon. (83-84)

The gene pool will become an *evolutionarily stable set* of genes, defined as a gene pool that cannot be invaded by any new gene. Most new genes that arise, either by mutation or reassortment or immigration, are quickly penalized by natural selection: the evolutionarily stable set is restored. Occasionally a new gene does succeed in invading the set: it succeeds in spreading through the gene pool there is a transitional period of instability, terminating in a new evolutionarily stable set – a little bit of evolution has occurred. By analogy with the aggression strategies, a population might have more than one alternative stable point, and it might occasionally flip from one to another. Progressive evolution may be not so much a steady upward climb as a series of discrete steps from stable plateau to stable plateau. It may look as though the population as a whole is behaving like a single self-regulating unit. But this illusion is produced by selection going on at the level of the single gene. Genes are selected on 'merit'. But merit is judged on the basis of performance against the background of the evolutionarily stable set which is the current gene pool. (86)

## CHAPTER 6 – GENESMANSHIP

What is the selfish gene? It is not just one single physical bit of DNA. Just as in the primeval soup, it is *all replicas* of a particular bit of DNA, distributed throughout the world. If we allow ourselves the license of talking about genes as if they had conscious aims, always reassuring ourselves that we could translate our sloppy language back into respectable terms if we wanted to, we can ask the question, what is a single selfish gene trying to do? It is trying to get more numerous in the gene pool basically it does this by helping to program the bodies in which it finds itself to survive and to reproduce. But now we are emphasizing that 'it' is a distributed agency, existing in many different individuals at once. The key point of this chapter is that a gene might be able to assist *replicas* of itself that are sitting in other bodies. If so, this would appear as individual altruism but it would be brought about by gene selfishness. (88)

We can now see that parental care is just a special case of kin altruism. Genetically speaking, an adult should devote just as much care and attention to its orphaned baby brother as it does to one of its own children. Its relatedness to both infants is exactly the same,  $\frac{1}{2}$ . In gene selection terms, a gene for big sister altruistic behaviour should have just as good a chance of spreading through the population as a gene for parental altruism. In practice, this is an over-simplification for various

reasons which we shall come to later, and brotherly or sisterly care is nothing like so common in nature as parental care. But the point I am making here is that there is nothing special *genetically* speaking about the parent / child relationship as against the brother / sister relationship. The fact that parents actually hand on genes to children, but sisters do not hand on genes to each other is irrelevant, since the sisters both receive identical replicas of the same genes from the same parents. (93-94)

Genetically speaking, parental care and brother / sister altruism evolve for exactly the same reason: in both cases there is a good chance that the altruistic gene is present in the body of the beneficiary. (94)

Grandparents and grandchildren have, genetically speaking, equal reason to behave altruistically to each other, since they share  $\frac{1}{4}$  of each other's genes. But if the grandchildren have the greater expectation of life, genes for grandparent to grandchildren altruism have a higher selective advantage than genes for grandchild to grandparent altruism. It is quite possible for the net benefit of assisting a young distant relative to exceed the net benefit of assisting an old close relative. (95)

In a species whose members do not move around much, or whose members move around in small groups, the chances may be good that any random individual you come across is fairly close kin to you. In this case the rule 'Be nice to any member of the species whom you meet' could have positive survival value, in the sense that a gene predisposing its possessors to obey the rule might become more numerous in the gene pool. This may be why altruistic behaviour is so frequently reported in troops of monkeys and schools of whales. Whales and dolphins drown if they are not allowed to breathe air. Baby whales, and injured individuals who cannot swim to the surface have been seen to be rescued and helped up by companions in the school. It is not known whether whales have ways of knowing who their close relatives are, but it is possible that it does not matter. It may be that the overall probability that a random member of the school is a relation is so high that the altruism is worth the cost. Incidentally, there is at least one well-authenticated story of a drowning human swimmer being rescued by a wild dolphin. This could be regarded as a misfiring of the rule for saving drowning member of the school. The rule's 'definition' of a member of the school who is drowning might be something like: 'A long thing thrashing about and choking near the surface.' (100)

So we conclude that the 'true' relatedness may be less important in the evolution of altruism than the best *estimate* of relatedness that animals can get. This fact is probably a key to understanding why parental care is so much more common and more devoted than brother / sister altruism in nature, and also why animals may value themselves more highly even than several brothers. Briefly, what I am saying is that, in addition to the index of relatedness, we should consider something like an index of 'certainty'. Although the parent / child relationship is no closer genetically than the brother / sister relationship, its certainty is greater. It is normally possible to be much more certain who your children are than who your brothers are. And you can be more certain still who you yourself are! (105)

## CHAPTER 7 – FAMILY PLANNING

It is easy to see why some people have wanted to separate parental care from the other kinds of kin-selected altruism. Parental care looks like an integral part of reproduction whereas, for example, altruism toward a nephew is not. I think there really is an important distinction hidden here, but that people have mistaken what the distinction is. They have put reproduction and parental care on one side, and other sorts of altruism on the other. But I wish to make a distinction between *bringing new individuals into the world*, on the one hand, and *caring for existing individuals* on the other. I shall call these two activities respectively child-bearing and child-caring.

An individual survival machine has to make two quite different sorts of decisions, caring decisions and bearing decisions. I use the world decision to mean unconscious strategic move. The caring decisions are of this form: 'There is a child; its degree of relatedness to me is so and so; its chances of dying if I do not feed it are such and such; shall I feed it?' Bearing decision, on the other hand, are like this: 'Shall I take whatever steps are necessary in order to bring a new individual into the world; shall I reproduce?' To some extent, caring and bearing are bound to compete with each other for an individual's time and other resources: the individual may have to make a choice: 'Shall I care for this child or shall I bear a new one?' (109)

We have probably all seen examples of the startling calculations that can be used to bring this [accelerating population growth spells serious trouble] home. For instance, the present population of Latin America is around 300 million, and already many of them are under-nourished. But if the population continued to increase at the present rate, it would take less than 500 years to reach the point where the people, packed in a standing position, formed a solid human carpet over the whole area of the continent. This is so, even if we assume them to be very skinny – a not unrealistic assumption. In 1,000 years from now they would be standing on each other's shoulders more than a million deep. By 2,000 years, the mountain of people, traveling outwards at the speed of light, would have reached the edge of the known universe.

It will not have escaped you that this is a hypothetical calculation! It will not really happen like that for some very good practical reasons. The names of some of these reasons are famine, plague, and war; *or*, if we are lucky, birth control. It is no use appealing to advances in agricultural science – 'green revolutions' and the like. Increases in food production may temporarily alleviate the problem, but it is mathematically certain that they cannot be a long-term solution; indeed, like the medical advances that have precipitated the crisis, they may well make the problem worse, by speeding up the rate of the population expansion. It is a simple logical truth that, short of mass emigration into space, with rockets taking off at the rate of several million per second, uncontrolled birth-rates are bound to lead to horribly increased death-rates. It is hard to believe that this simple truth is not understood by those leaders who forbid their followers to use effective contraception methods. They express a preference for 'natural' methods of population limitation, and a natural method is exactly what they are going to get. It is called starvation. (111)

Wild animals almost never die of old age: starvation, disease, or predators catch up with them long before they become really senile. (112)

Contraception is sometimes attacked as 'unnatural'. So it is, very unnatural. The trouble is, so is the welfare state. I think that most of us believe that welfare state is highly desirable. But you cannot have an unnatural welfare state, unless you also have unnatural birth-control, otherwise the end result will be misery even greater than that which obtains in nature. The welfare state is perhaps the greatest altruistic system the animal kingdom has ever known. But any altruistic system is inherently unstable, because it is open to abuse by selfish individuals, ready to exploit it. Individual humans who have more children than they are capable of rearing are probably too ignorant in most cases to be accused of conscious malevolent exploitation. Powerful institutions and leaders who deliberately encourage them to do so seem to me less free from suspicion. (117-118)

Our conclusion from this chapter is that individual parents practise family planning, but in the sense that they optimize their birth-rates rather than restrict them for public good. They try to maximize the number of surviving children that they have, and this means having neither too many babies nor too few. Genes that make an individual have too many babies tend not to persist in the gene pool, because children containing such genes tend not to survive to adulthood. (122)

## CHAPTER 8 – BATTLE OF THE GENERATIONS

Parental Investment (P.I.) [conceptualized by R. L. Trivers in 1972] is defined as 'any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring'. The beauty of Trivers's parental investment is that it is measured in units very close to the units that really matter. When a child uses up some of its mother's milk, the amount of milk consumed is measured not in pints, not in calories, but in units of detriment to other children of the same mother. For instance, if a mother has two babies, X and Y, and X drinks one pint of milk, a major part of the P.I. That this pint represents is measured in units of increased probability that Y will die because he did not drink that pint. P.I. Is measured in units of decrease in life expectancy of other children, born or yet to be born.

Parental investment is not quite an ideal measure, because it overemphasizes the importance of parentage, as against other genetic relationships. Ideally we should use a generalized *altruism investment* measure. Individual A may be said to invest in individual B, when A increases B's chance of surviving, at the cost of A's ability to invest in other individuals including herself, all costs being weighted by the appropriate relatedness. Thus a parent's investment in any one child should ideally be measured in terms of detriment to life expectancy not only of other children, but also of nephews, nieces, herself, etc. in many respects, however, this is just a quibble, and Trivers's measure is well worth using in practice. (124)

This seems a good moment to mention the puzzling phenomenon known as the menopause, the rather abrupt termination of a human female's reproductive fertility in middle age. This may not have occurred too commonly in our wild ancestors, since not many women would have lived that long anyway. But still, the difference between the abrupt change of life in women and the gradual fading out of fertility in men suggests that there is something genetically 'deliberate' about the menopause – that it is an 'adaptation'. It is rather difficult to explain. At first sight we might expect that a woman should go on having children until she dropped, even if advancing years made it progressively less likely that any individual child would survive. Surely it would seem always worth trying? But we must remember that she is also related to her grandchildren, though half as closely.

For various reasons, perhaps connected with the Medawar theory of aging [...], women in the natural state became gradually less efficient at bringing up children as they got older. Therefore the life expectancy of a child of an old mother was less than that of a child of a young mother. This means that, if a woman had a child and a grandchild born on the same day, the grandchild could expect to live longer than the child. When a woman reached the age where the average chance of each child reaching adulthood was just less than half the chance of each grandchild of the same age reaching adulthood, any gene for investing in grandchildren in preference to children would tend to prosper. Such a gene is carried by only one in four grandchildren, whereas the rival gene is carried by one in two children, but the greater expectation of life of the grandchildren outweighs this, and the 'grandchild altruism' gene prevails in the gene pool. A woman could not invest fully in her grandchildren if she went on having children of her own. Therefore genes for becoming reproductively infertile in middle age became more numerous, since they were carried in the bodies of grandchildren whose survival was assisted by grandmotherly altruism.

This is a possible explanation of the evolution of the menopause in females. The reason why the fertility of males tails off gradually rather than abruptly is probably that males do not invest so much as females in each individual child anyway. Provided he can sire children by young women, it will always pay even a very old man to invest in children rather than in their grandchildren. (126-127)

A mother is equally related to all her children, born and to be born. On genetic grounds alone she should have no favourites, as we have seen. If she does show favouritism it should be based on differences in expectation of life, depending on age and other things. The mother, like

any individual, is twice as closely 'related' to herself as she is to any of her children. Other things being equal, this means that she should invest most of her resources selfishly in herself, but other things are not equal. She can do her genes more good by investing a fair proportion of her resources in her children. This is because these are younger and more helpless than she is, and they can therefore benefit more from each unit of investment than she can herself. Genes for investing in more helpless individuals in preference to oneself can prevail in the gene pool, even though the beneficiaries may share only a portion of one's genes. This is why animals show parental altruism, and indeed why they show any kind of kin-selected altruism.

Now look at it from the point of view of a particular child. He is just as closely related to each of his brothers and sisters as his mother is to them. The relatedness is  $\frac{1}{2}$  in all cases. Therefore he 'wants' his mother to invest some of her resources in his brothers and sisters. Genetically speaking, he is just as altruistically disposed to them as his mother is. But again, he is twice as closely related to himself as he is to any brother or sister, and this will dispose him to want his mother to invest in him more than in any particular brother or sister, other things being equal. In this case other things might indeed be equal. If you and your brother are the same age, and both are in a position to benefit equally from a pint of mother's milk, you 'should' try to grab more than your fair share, and he should try to grab more than his fair share. Have you ever heard a litter of piglets squealing to be first on the scene when the mother sow lies down to feed them? Or little boys fighting over the last slice of cake? Selfish greed seems to characterize much of child behaviour.

But there is more to it than this. If I am competing with my brother for a morsel of food, and if he is much younger than me so that he could benefit from the food more than I could, it might pay my genes to let him have it. An elder brother may have exactly the same grounds for altruism as a parent: in both cases, as we have seen, the relatedness is  $\frac{1}{2}$ , and in both cases the younger individual can make better use of the resource than the elder. If I possess a gene for giving up food, there is a 50 per cent chance that my baby brother contains the same gene. Although the gene has double the chance of being in my own body – 100 per cent, it *is* in my body – my need of the food may be less than half as urgent. In general, a child 'should' grab more than his share of parental investment, but only up to a point. Up to what point? Up to the point where the resulting net cost to his brothers and sisters, born and potentially to be born, is just double the benefit of the grabbing to himself. (127-128)

... there are honeyguides who, like cuckoos, lay their eggs in the nest of other species. The baby honeyguide is equipped with a sharp, hooked beak. As soon as he hatches out, while he is still blind, naked, and otherwise helpless, he scythes and slashes his foster brothers and sisters to death: dead brothers do not compete for food! The familiar British cuckoo achieves the same result in a slightly different way. It has a short incubation-time, and so the baby cuckoo manages to hatch out before its foster brothers and sisters. As soon as it hatches, blindly and mechanically, but with devastating effectiveness, it throws the other eggs out of the nest. It gets underneath an egg, fitting it into a hollow in its back. Then it slowly backs up the side of the nest, balancing the egg between its wing-stubs, and topples the egg out on to the ground. It does the same with all the other eggs, until it has the nest, and therefore the attention of its foster parents, entirely to itself. (133)

Genes are selected for their ability to make the best use of the levers of power at their disposal: they will exploit their practical opportunities. When a gene is sitting in a juvenile body its practical opportunities will be different from when it is sitting in a parental body. Therefore its optimum policy will be different in the two stages in its body's life history. (137)

If there is a human moral to be drawn, it is that we must *teach* our children altruism, for we cannot expect it to be part of their biological nature. (139)

## CHAPTER 9 – BATTLE OF THE SEXES

But what is the essence of maleness? What, at bottom, defines a female? We as mammals see the sexes defined by whole syndromes of characteristics – possession of a penis, bearing of the young, suckling by means of special milk glands, certain chromosomal features, and so on. These criteria for judging the sex of an individual are all very well for mammals but, for animals and plants generally, they are no more reliable than is the tendency to wear trousers as a criterion for judging human sex. In frogs, for instance, neither sex has a penis. Perhaps, then, the words male and female have no general meaning. They are, after all, only words, and if we do not find them helpful for describing frogs, we are quite at liberty to abandon them. We could arbitrarily divide frogs into Sex 1 and Sex 2 if we wished. However, there is one fundamental feature of the sexes which can be used to label males as males, and females as females, throughout animals and plants. This is that the sex cells or 'gametes' of males are much smaller and more numerous than the gametes of females. This is true whether we are dealing with animals or plants. One group of individuals has large sex cells, and it is convenient to use the word female for them. The other group, which it is convenient to call male, has small sex cells. The difference is especially pronounced in reptiles and in birds, where a single egg cell is big enough and nutritious enough to feed a developing baby for several weeks. Even in humans, where the egg is microscopic, it is still many times larger than the sperm. As we shall see, it is possible to interpret all the other differences between the sexes as stemming from this one basic difference.

In certain primitive organisms, for instance some fungi, maleness and femaleness do not occur, although sexual reproduction of a kind does. In the system known as isogamy the individuals are not distinguishable into two sexes. Anybody can mate with anybody else. There are not two different sorts of gametes – sperms and eggs – but all sex cells are the same, called isogametes. New individuals are formed by the fusion of two isogametes, each produced by meiotic division. If we have three isogametes, A, B, and C, A could fuse with B or C, B could fuse with A or C. The same is never true of normal sexual systems. If A is a sperm and it can fuse with B or C, then B and C must be eggs and B cannot fuse with C.

When two isogametes fuse, both contribute equal numbers of genes to the new individual, and they also contribute equal amounts of food reserves. Sperms and eggs too contribute equal numbers of genes, but eggs contribute far more in the way of food reserves: indeed, sperms make no contribution at all and are simply concerned with transporting their genes as fast as possible to an egg. At the moment of conception, therefore, the father has invested less than his fair share (i.e. 50 per cent) of resources in the offspring. Since each sperm is so tiny, a male can afford to make many millions of them every day. This means he is potentially able to beget a very large number of children in a very short period of time, using different females. This is only possible because each new embryo is endowed with adequate food by the mother in each case. This therefore places a limit on the number of children a female can have, but the number of children a male can have is virtually unlimited. Female exploitation begins here. (141-142)

Males, then, seem to be pretty worthless fellows, and on simple 'good of the species' grounds, we might expect that males would become less numerous than females. Since one male can theoretically produce enough sperms to service a harem of 100 females we might suppose that females should outnumber males in animal populations by 100 to 1. Other ways of putting this are that the male is more 'expendable', and the female more 'valuable' to the species. Of course, looked at from the point of view of the species as a whole, this is perfectly true. To take an extreme example, in one study of elephant seals, 4 per cent of the males accounted for 88 per cent of all the copulations observed. In this case, and in many others, there is a large surplus of bachelor males who probably never get a chance to copulate in their whole lives. But these extra males live otherwise normal lives, and they eat up the population's food resources no less hungrily than other adults. From a 'good of the species' point of view this is horribly wasteful; the extra males might be regarded as social parasites. This is just one more example of the difficulties that the group selection theory gets into. The selfish gene theory, on the other hand, has no trouble in

explaining the fact that the numbers of males and females tend to be equal, even when the males who actually reproduce may be a small fraction of the total number. (143)

... Bruce effect: male mice secrete a chemical which when smelt by a pregnant female can cause her to abort. She only aborts if the smell is different from that of her former mate. In this way a male mouse destroys his potential step-children, and renders his new wife receptive to his own sexual advances. [...] A similar example is that of male lions, who, when newly arrived in a pride, sometimes murder existing cubs, presumably because these are not their own children. (147)

... the various different kinds of breeding systems that we find among animals – monogamy, promiscuity, harems, and so on – can be understood in terms of conflicting interests between males and females. Individuals of either sex 'want' to maximize their total reproductive output during their lives. Because of a fundamental difference between the size and numbers of sperms and eggs, males are in general likely to be biased towards promiscuity and lack of parental care. Females have two main available counter-ploys, which I have called the he-man [male procreates and deserts] and the domestic-bliss [male procreates and sticks around] strategies. The ecological circumstances of a species will determine whether the females are biased towards one or the other of these counter-ploys, and will also determine how the males respond. In practice all intermediates between he-man and domestic bliss are found and, as we have seen, there are cases in which the father does even more child-care than the mother. (161)

... it is strongly to be expected on evolutionary grounds that, where the sexes differ, it should be the males that advertise and the females that are drab. Modern western man is undoubtedly exceptional in this respect. It is of course true that some men dress flamboyantly and some women dress drably but, on average, there can be no doubt that in our society the equivalent of the peacock's tail is exhibited by the female, not by the male. Women paint their faces and glue on false eyelashes. Apart from special cases, like actors, men do not. Women seem to be interested in their own personal appearance and they are encouraged in this by their magazines and journals. Men's magazines are less preoccupied with male sexual attractiveness, and a man who is unusually interested in his own dress and appearance is apt to arouse suspicion, both among men and among women. When a woman is described in conversation, it is quite likely that her sexual attractiveness, or lack of it, will be prominently mentioned. This is true, whether the speaker is a man or a woman. When a man is described, the adjectives used are much more likely to have nothing to do with sex.

Faced with these facts, a biologist would be forced to suspect that he was looking at a society in which females compete for males, rather than vice versa. In the case of birds of paradise, we decided that females are drab because they do not need to compete for males. Males are bright and ostentatious because females are in demand and can afford to be choosy. The reason female birds of paradise are in demand is that eggs are a more scarce resources than sperms. What has happened in modern western man? Has the male really become the sought-after sex, the one that is in demand, the sex that can afford to be choosy? If so, why?

## CHAPTER 10 – YOU SCRATCH MY BACK, I'LL RIDE ON YOURS

The other example that I said I would return to is the case of the kamikaze bees, who sting honey-raiders but commit almost certain suicide in the process. The honey bee is just one example of a highly *social* insect. Others are wasps, ants, and termites or 'white ants'. I want to discuss social insects generally, not just suicidal bees. The exploits of the social insects are legendary, in particular their astonishing feats of cooperation and apparent altruism. Suicidal stinging missions typify their prodigies of self-abnegation. In the 'honey-pot' ants there is a caste of workers with grotesquely swollen, food-packed abdomens, whose sole function in life is to hang motionless from the ceiling like bloated light-bulbs, being used as food stores by the other workers. In the human

sense they do not live as individuals at all; their individuality is subjugated, apparently to the welfare of the community. A society of ants, bees or termites achieves a kind of individuality at a higher level. Food is shared to such an extent that one may speak of a communal stomach. Information is shared so efficiently by chemical signals and by the famous 'dance' of the bees that the community behaves almost as if it were a unit with a nervous system and sense organs of its own. Foreign intruders are recognized and repelled with something of the selectivity of a body's immune reaction system. The rather high temperature inside a beehive is regulated nearly as precisely as that of the human body, even though an individual bee is not a 'warm blooded' animal. Finally and most importantly, the analogy extends to reproduction. The majority of individuals in a social insect colony are sterile workers. The 'term line' – the line of immortal gene continuity – flows through the bodies of a minority of individuals, the reproductives. These are the analogues of our own reproductive cells in our testes and ovaries. The sterile workers are the analogy of our liver, muscle, and nerve cells.

Kamikaze behaviour and other forms of altruism and cooperation by workers are not astonishing once we accept the fact that they are sterile. The body of a normal animal is manipulated to ensure the survival of its genes both through bearing offspring and through caring for other individuals containing the same genes. Suicide in the interests of caring for other individuals is incompatible with future bearing of one's own offspring. Suicidal self-sacrifice therefore seldom evolves. But a worker bee never bears offspring of its own. All its efforts are directed to preserving its genes by caring for relatives other than its own offspring. The death of a single sterile worker bee is no more serious to its genes than is the shedding of a leaf in autumn to the genes of a tree. (171-172)

True warfare in which large rival armies fight to the death is known only in man and in social insects. In many species of ants the specialized caste of workers known as soldiers have formidable fighting jaws, and devote their time to fighting for the colony against other ant armies. Slaving raids are just a particular kind of war effort. The slavers mount an attack on a nest of ants belonging to a different species, attempt to kill the defending workers or soldiers, and carry off the unhatched young. These young ones hatch out in the nest of their captors. They do not 'realize' that they are slaves and they set to work following their built-in nervous programs, doing all the duties that they would normally perform in their own nest. The slave-making workers or soldiers go on further slaving expeditions while the slaves stay at home and get on with the everyday business of running an ants' nest, cleaning, foraging, and caring for the brood.

The slaves are, of course, blissfully ignorant of the fact that they are unrelated to the queen and to the brood that they are tending. Unwittingly they are rearing new platoons of slave-makers. No doubt natural selection, acting on the genes of the slave species, tends to favour anti-slavery adaptations. However, these are evidently not fully effective because slavery is a wide spread phenomenon. (177-178)

... several species of ants in the New World, and, quite independently, termites in Africa, cultivate 'fungus gardens'. The best known are the so-called parasol ants of South America. These are immensely successful. Single colonies with more than two million individuals have been found. Their nests consist of huge spreading underground complexes of passages and galleries going down to a depth of ten feet or more, made by the excavation of as much as 40 tons of soil. The underground chambers contain the fungus gardens. The ants deliberately sow fungus of a particular species in special compost beds with they prepare by chewing leaves into fragments. Instead of foraging directly for their own food, the workers forage the leaves to make compost. The 'appetite' of a colony of parasol ants for leaves is gargantuan. This makes them a major economic pest, but the leaves are not food for themselves but food for their fungi. The ants eventually harvest and eat the fungi and feed them to their brood. The fungi are more efficient at breaking down leaf material than the ants' own stomachs would be, which is how the ants benefit by the arrangement. It is possible that the fungi benefit too, even though they are cropped: the ants propagate them more efficiently than their own spore dispersal mechanism might achieve.

Furthermore, the ants 'weed' the fungus gardens, keeping them clear of alien species of fungi. By removing competition, this may benefit the ants' own domestic fungi. A kind of relationship of mutual altruism could be said to exist between ants and fungi. It is remarkable that a very similar system of fungus-farming has evolved independently, among the quite unrelated termites.

Ants have their own domestic animals as well as their crop plants. Aphids – greenfly and similar bugs – are highly specialized for sucking the juice out of plants. They pump the sap up out of the plants' veins more efficiently than they subsequently digest it. The result is that they excrete a liquid that has had only some of its nutritious value extracted. Droplets of sugar-rich 'honeydew' pass out of the back end at a great rate, in some cases more than the insect's own body-weight every hour. The honeydew normally rains down on to the ground – it may well have been the providential food known as 'manna' in the Old Testament. But ants of several species intercept it as soon as it leaves the bug. The ants 'milk' the aphids by stroking their hind-quarters with their feelers and legs. Aphids respond to this, in some cases apparently holding back their droplets until an ant strokes them, and even withdrawing a droplet if an ant is not ready to accept it. It has been suggested that some aphids have evolved a backside that looks and feels like an ant's face, the better to attract ants. What the aphids have to gain from the relationship is apparently protection from their natural enemies. Like our own dairy cattle they lead a sheltered life, and aphid species that are much cultivated by ants have lost their normal defensive mechanisms. In some cases ants care for the aphid eggs inside their own underground nests, feed the young aphids, and finally, when they are grown, gently carry them up to the protected grazing grounds. (180-181)

Within each one of our cells there are numerous tiny bodies called mitochondria. The mitochondria are chemical factories, responsible for providing most of the energy we need. If we lost our mitochondria we would be dead within seconds. Recently it has been plausibly argued that mitochondria are, in origin, symbiotic bacteria who joined forces with our type of cell very early in evolution. Similar suggestions have been made for other small bodies within our cells. This is one of those revolutionary ideas which it takes time to get used to, but it is an idea whose time has come. I speculate that we shall come to accept the more radical idea that each one of our genes is a symbiotic unit. We are gigantic colonies of symbiotic genes. One cannot really speak of 'evidence' for this idea, but, as I tried to suggest in earlier chapters, it is really inherent in the very way we think about how genes work in sexual species. The other side of this coin is that viruses may be genes who have broken loose from 'colonies' such as ourselves. Viruses consist of pure DNA (or a related self-replicating molecule) surrounded by a protein jacket. They are all parasitic. The suggestion is that they have evolved from 'rebel' genes who escaped, and now travel from body to body directly through the air, rather than via the more conventional vehicles – sperms and eggs. If this is true, we might just as well regard ourselves as colonies of viruses! Some of them cooperate symbiotically, and travel from body to body in sperms and eggs. These are the conventional 'genes'. Others live parasitically, and travel by whatever means they can. If the parasitic DNA travels in sperms and eggs, it perhaps forms the 'paradoxical' surplus of DNA [...]. if it travels through the air, or by other direct means, it is called 'virus' in the usual sense. (182)

Cleaner-fish have special stripy patterns and special dancing displays which label them as cleaners. Large fish tend to refrain from eating small fish who have the right kind of stripes, and who approach them with the right kind of dance. Instead they go into a trance-like state and allow the cleaner free access to their exterior and interior. Selfish genes being what they are, it is not surprising that ruthless, exploiting cheats have cashed in. there are species of small fish that look just like cleaners and dance in the same kind of way in order to secure safe conduct into the vicinity of large fish. When the large fish has gone into its expectant trance the the cheat, instead of pulling off a parasite, bites a chunk out of the large fish's fin and beats a hasty retreat. But in spite of the cheats, the relationship between fish cleaners and their clients is mainly amicable and stable. The profession of cleaner plays an important part in the daily life of the coral reef community. Each cleaner has his own territory, and large fish have been seen queuing up for attention like customers at a barber's shop. It is probably this site-tenacity that makes possible the

evolution of delayed reciprocal-altruism in this case. The benefit to a large fish of being able to return repeatedly to the same 'barber's shop', rather than continually searching for a new one, must outweigh the cost of refraining from eating the cleaner. Since cleaners are small, this is not hard to believe. The presence of cheating cleaner-mimics probably indirectly endangers the bonafide cleaners by setting up a minor pressure on large fish to eat stripy dancers. Site-tenacity on the part of genuine cleaners enables customers to find them and to avoid cheats.

A long memory and a capacity for individual recognition are well developed in man. We might therefore expect reciprocal altruism to have played an important part in human evolution. Trivers goes so far as to suggest that many of our psychological characteristics – envy, guilt, gratitude, sympathy etc. - have been shaped by natural selection for improved ability to cheat, to detect cheats, and to avoid being thought to be a cheat. Of particular interest are 'subtle cheats' who appear to be reciprocating, but who consistently pay back slightly less than they receive. It is even possible that man's swollen brain, and his predisposition to reason mathematically, evolved as a mechanism of ever more devious cheating, and ever more penetrating detection of cheating in others. Money is a formal token of delayed reciprocal altruism. (187-188)

## CHAPTER 11 – MEMES; THE NEW REPLICATORS

Most of what is unusual about man can be summed up in one word: 'culture'. I use the word not in its snobbish sense, but as a scientist uses it. Cultural transmission is analogous to genetic transmission in that, although basically conservative, it can give rise to a form of evolution. Geoffrey Chaucer could not hold a conversation with a modern Englishman, even though they are linked to each other by an unbroken chain of some twenty generations of Englishmen, each of whom could speak to his immediate neighbours in the chain as a son speaks to his father. Language seems to 'evolve' by non-genetic means, and at a rate which is orders of magnitude faster than genetic evolution.

Cultural transmission is not unique to man. The best non-human example that I know has recently been described by P. F. Jenkins in the song of a bird called the saddleback which lives on an island off New Zealand. On the island where he worked there was a total repertoire of about nine distinct songs. The males could be classified into dialect groups. For example, one group of eight males with neighboring territories sang a particular song called the CC song. Other dialect groups sang different songs. Sometimes the members of a dialect group shared more than one distinct song. By comparing the songs of fathers and sons, Jenkins showed that song patterns were not inherited genetically. Each young male was likely to adopt songs from his territorial neighbours by imitation, in an analogous way to human language. During most of the time Jenkins was there, there was a fixed number of songs on the island, a kind of 'song pool' from which each young male drew his own small repertoire. But occasionally Jenkins was privileged to witness the 'invention' of a new song, which occurred by a mistake in the imitation of an old one. He writes: 'New song forms have been shown to arise variously by change of pitch of a note, repetition of a note, the elision of notes and the combination of parts of other existing songs ... The appearance of the new form was an abrupt event and the product was quite stable over a period of years. Further, in a number of cases the variant was transmitted accurately in its new form to younger recruits so that a recognizably coherent group of like singers developed.' Jenkins refers to the origins of new songs as 'cultural mutations'. (189-190)

The laws of physics are supposed to be true all over the accessible universe. Are there any principles of biology that are likely to have similar universal validity? When astronauts voyage to distant planets and look for life, they can expect to find creatures too strange and unearthly for us to imagine. But is there anything that must be true of all life, wherever it is found, and whatever the basis of its chemistry? If forms of life exist whose chemistry is based on silicon rather than carbon, or ammonia rather than water, if creatures are discovered that boil to death at -100 degrees centigrade, if a form of life is found that is not based on chemistry at all but on electronic

reverberating circuits, will there still be any general principle that is true of all life? Obviously I do not know but, if I had to bet, I would put my money on one fundamental principle. This is the law that all life evolves by the differential survival of replicating entities. The gene, the DNA molecule, happens to be the replicating entity that prevails on our own planet. There may be others. If there are, provided certain other conditions are met, they will almost inevitably tend to become the basis for an evolutionary process.

But do we have to go to distant worlds to find other kinds of replicator and other, consequent, kinds of evolution? I think that a new kind of replicator has recently emerged on this very planet. It is staring us in the face. It is still in its infancy, still drifting clumsily about in its primeval soup, but already it is achieving evolutionary change at a rate that leaves the old gene panting far behind.

The new soup is the soup of human culture. We need a name for the new replicator, a noun that conveys the idea of a unit of cultural transmission, or a unit of *imitation*. 'Mimeme' comes from a suitable Greek root, but I want a monosyllable that sounds a bit like 'gene'. I hope my classicist friends will forgive me if I abbreviate mimeme to *meme*. If it is any consolation, it could alternatively be thought of as being related to 'memory', or to the French word for *même*. It should be pronounced to rhyme with 'cream'. (191-192)

Consider the idea of God. We do not know how it arose in the meme pool. Probably it originated many times by independent 'mutation'. In any case, it is very old indeed. How does it replicate itself? By the spoken and written word, aided by great music and great art. Why does it have such high survival value? Remember that 'survival value' here does not mean value for a gene in a gene pool, but value for a meme in a meme pool. This question really means: What is it about the idea of a god that gives it its stability and penetrance in the cultural environment? The survival value of the god meme in the meme pool results from its great psychological appeal. It provides a superficially plausible answer to deep and troubling questions about existence. It suggests that injustices in this world may be rectified in the next. The 'everlasting arms' hold out a cushion against our own inadequacies which, like a doctor's placebo, is none the less effective for being imaginary. These are some of the reasons why the idea of God is copied so readily by successive generations of individual brains. God exists, if only in the form of a meme with high survival value, or ineffective power, in the environment provided by human culture. (192-193)

To take a particular example, an aspect of doctrine that has been very effective in enforcing religious observance is the threat of hell fire. Many children and even some adults believe that they will suffer ghastly torments after death if they do not obey the priestly rules. This is a peculiarly nasty technique of persuasion, causing great psychological anguish throughout the middle ages and even today. But it is highly effective. It might almost have been planned deliberately by a Machiavellian priesthood trained in deep psychological indoctrination techniques. However, I doubt if the priests were that clever. Much more probably, unconscious memes have ensured their own survival by virtue of those same qualities of pseudo-ruthlessness that successful genes display. The idea of hell fire is, quite simply *self-perpetuating*, because of its own deep psychological impact. It has become linked with the god meme because the two reinforce each other, and assist each other's survival in the meme pool.

Another member of the religious meme complex is called faith. It means blind trust, in the absence of evidence, even in the teeth of evidence. The story of doubting Thomas is told, not so that we shall admire Thomas, but so that we can admire the other apostles in comparison. Thomas demanded evidence. Nothing is more lethal for certain kinds of meme than a tendency to look for evidence. The other apostles, whose faith was so strong that they did not need evidence, are held up to us as worthy of imitation. The meme for blind faith secures its own perpetuation by the simple unconscious expedient of discouraging rational inquiry.

Blind faith can justify anything. If a man believes in a different god, or even if he uses a different ritual for worshiping the same god. Blind faith can decree that he should die – on the cross, at the stake, skewered on a Crusader's sword, shot in a Beirut street, or blown up in a bar

in Belfast. Memes for blind faith have their own ruthless ways of propagating themselves. This is true of patriotic and political as well as religious blind faith. (197-198)

## CHAPTER 12 – NICE GUYS FINISH FIRST

This talk of laughing all the way to the bank reminds me of a delightful line from Shakespeare:

*The first thing we do, let's kill all the lawyers.*

*2 Henry VI*

In what are called civil 'disputes' there is often in fact great scope for cooperation. What looks like a zero sum confrontation can, with a little goodwill, be transformed into a mutually beneficial nonzero sum game. Consider divorce. A good marriage is obviously a nonzero sum game, brimming with mutual cooperation. But even when it breaks down there are all sorts of reason why a couple could benefit by continuing to cooperate, and treating their divorce, too, as nonzero sum. As if child welfare were not a sufficient reason, the fees of two lawyers will make a nasty dent in the family finances. So obviously a sensible and civilized couple begin by going *together* to see one lawyer, don't they?

Well, actually no. At least in England and, until recently, in all fifty states of the USA, the law, or more strictly – and significantly the lawyers' own professional code, doesn't allow them to. Lawyers must accept only one member of a couple as a client. The other person is turned from the door, and either has no legal advice at all or is forced to go to another lawyer. And that is when the fun begins. In separate chambers but with one voice, the two lawyers immediately start referring to 'us' and 'them'. 'Us', you understand, doesn't mean me and my wife; it means me and my lawyer against her and her lawyer. When the case comes to court, it is actually listed as 'Smith *versus* Smith'! It is *assumed* to be adversarial, whether the couple feel adversarial or not, whether or not they have specifically agreed that they want to be sensibly amicable. And who benefits from treating it as an 'I win, you lose' tussle? The chances are, only the lawyers.

The hapless couple have been dragged into a zero sum game. For the lawyers, however, the case of *Smith v. Smith* is a nice fat *nonzero* sum game, with the Smiths providing the payoffs and the two professionals milking their clients' joint account in elaborately coded cooperation. One way in which they cooperate is to make proposals that they both know that the other side will not accept. This prompts a counter proposal that, again, both know is unacceptable. And so it goes on. Every letter, every telephone call exchanged between the cooperating 'adversaries' adds another wad to the bill. With luck, this procedure can be dragged out for months or even years, with costs mounting in parallel. The lawyers don't get together to work all this out. On the contrary, it is ironically their scrupulous separateness that is the chief instrument of their cooperation at the expense of the clients. The lawyers may not even be aware of what they are doing. Like the vampire bats [...] they are playing to well-ritualized rules. It is all geared to forcing us into zero sum games. Zero sum for the clients, but very much *nonzero* sum for the lawyers. (221-222)

It is quite well known that at Christmas British and German troops briefly fraternized and drank together in no-man's-land. Less well known, but in my opinion more interesting, is the fact that unofficial and unspoken nonaggression pacts, a 'live-and-let-live' system, flourished all up and down the front lines for at least two years starting in 1914. A senior British officer, on a visit to the trenches, is quoted as being astonished to observe German soldiers walking about within rifle range behind their own line. 'Our men appeared to take no notice. I privately made up my mind to do away with that sort of thing when we took over; such thing should not be allowed. These people evidently did not know there was a war on. Both sides apparently believed in the policy of "live-and-let-live".' (225)

Fig trees and fig wasps share an intimate cooperative relationship. The fig that you eat is not really a fruit. There is a tiny hole at the end, and if you go into this hole (you'd have to be as small as a

fig wasp to do so, and they are minute: thankfully too small to notice when you eat a fig), you find hundreds of tiny flowers lining the walls. The fig is a dark indoor hothouse for flowers, an indoor pollination chamber. And the only agents that can do the pollinating are fig wasps. The tree, then, benefits from harbouring the wasps. But what is in it for the wasps? They lay their eggs in some of the tiny flowers, which the larvae then eat. They pollinate other flowers within the same fig. 'Defecting', for a wasp, would mean laying eggs in too many of the flowers in a fig and pollinating too few of them. But how could a fig tree 'retaliate'? According to Axelrod and Hamilton, 'It turns out in many cases that if a fig wasp entering a young fig does not pollinate enough flowers for seeds and instead lays egg in almost all, the tree cuts off the developing fig at an early stage. All progeny of the wasp then perish.'

A bizarre example of what appears to be a Tit for Tat arrangement in nature was discovered by Eric Fischer in a hermaphrodite fish, the sea bass. Unlike us, these fish don't have their sex determined at conception by their chromosomes. Instead, every individual is capable of performing both female and male functions. In any one spawning episode they shed either eggs or sperm. They form monogamous pairs and, within the pair, take turns to play the male and female roles. Now, we may surmise that any individual fish, if it could get away with it, would 'prefer' to play the male role all the time, because the male role is cheaper. Putting it another way, an individual that succeeded in persuading its partner to play the female most of the time would gain all the benefits of 'her' economic investment in eggs, while 'he' has resources left over to spend on other things, for instance on mating with other fish.

In fact, what Fischer observed was that the fishes operate a system of pretty strict alternation. This is just what we should expect if they are playing Tit for Tat. And it is plausible that they should, because it does appear that a game is a true Prisoner's Dilemma, albeit a somewhat complicated one. To play the COOPERATE card means to play the female role when it is your turn to do so. Attempting to play the male role when it is your turn to play the female is equivalent to playing the DEFECT card. Defection is vulnerable to retaliation: the partner can refuse to play the female role next time it is 'her' (his?) turn to do so, or 'she' can simply terminate the whole relationship. Fischer did indeed observe that pairs with an uneven sharing of sex roles tended to break up. (229-230)

## CHAPTER 13 – THE LONG REACH OF THE GENE

An uneasy tension disturbs the heart of the selfish gene theory. It is the tension between gene and individual body as fundamental agent of life. On the one hand we have the beguiling image of independent DNA replicators, skipping like chamois, free and untrammelled survival machines, immortal coils shuffling off an endless succession of mortal ones as they forge towards their separate eternities. On the other hand we look at the individual bodies themselves and each one is obviously a coherent, integrated, immensely complicated machine, with a conspicuous unity of purpose. A body doesn't *look* like the product of a loose and temporary federation of warring genetic agents who hardly have time to get acquainted before embarking in sperm or egg for the next leg of the great genetic diaspora. It has one single-minded brain which coordinates a cooperative of limbs and sense organs to achieve one end. The body looks and behaves like a pretty impressive agent in its own right. (234)

Darwinians have usually chosen to discuss genes whose phenotypic effects benefit, or penalize, the survival and reproduction of whole bodies. They have tended not to consider benefits to the gene itself. This is partly why the paradox at the heart of the theory doesn't normally make itself felt. For instance a gene may be successful through improving the running speed of a predator. The whole predator's body, including all its genes, is more successful because it runs faster. Its speed helps it survive to have children; and therefore more copies of all its genes, including the gene for fast running, are passed on. Here the paradox conveniently disappears because what is good for one gene is good for all. (235)

Questions about life are conventionally about organisms. Biologists ask why organisms do this, why organisms do that. They frequently ask why organisms group themselves into societies. They don't ask – though they should – why living matter groups itself into organisms in the first place. Why isn't the sea still a primordial battleground of free and independent replicators? Why did the ancient replicators club together to make, and reside in, lumbering robots, and why are those robots – individual bodies, you and me – so large and so complicated? (237)

The phenotypic effect of a gene are normally seen as all the effects that it has on the body in which it sits. This is the conventional definition. But we shall now see that the phenotypic effects of a gene need to be thought of as *all the effects that it has on the world*. It may be that a gene's effects, as a matter of fact, turn out to be confined to the succession of bodies in which the gene sits. But, if so, it will be just as a matter of fact. It will not be something that ought to be part of our very definition. In all this, remember that the phenotypic effects of a gene are the tools by which it levers itself into the next generation. All that I am going to add is that the tools may reach outside the individual body wall. What might it mean in practice to speak of a gene as having an extended phenotypic effect on the world outside the body in which it sits? Examples that spring to mind are artefacts like beaver dams, bird nests and caddis houses.

Caddis flies are rather nondescript, drab brown insects, which most of us fail to notice as they fly rather clumsily over rivers. That is when they are adults. But before they emerge as adults they have a rather longer incarnation as larvae walking about the river bottom. And caddis larvae are anything but nondescript. They are among the most remarkable creatures on earth. Using cement of their own manufacture, they skilfully build tubular houses for themselves out of materials that they pick up from the bed of the stream. The house is a mobile, carried about as the caddis walks, like the shell of a snail or hermit crab except that the animal builds it instead of growing it or finding it. Some species of caddis use sticks as building materials, others fragments of dead leaves, others small snail shells. But perhaps the most impressive caddis houses are the ones built in local stone. The caddis chooses its stones carefully, rejecting those that are too large or too small for the current gap in the wall, even rotating each stone until it achieves the snug fit. (238)

Parasites of all types have long been known to exert fascinatingly insidious influences on their hosts. A species of microscopic protozoan parasite called *Nosema*, which infests the larvae of flour beetles, has 'discovered' how to manufacture a chemical that is very special for the beetles. Like other insects, these beetles have a hormone called the juvenile hormone which keeps larvae as larvae. The normal change from larva to adult is triggered by the larva ceasing production of juvenile hormone. The parasite *Nosema* has succeeded in synthesizing (a close chemical analogue of) this hormone. Millions of *Nosema* club together to mass-produce juvenile hormone in the beetle larva's body, thereby preventing it from turning into an adult. Instead it goes on growing, ending up as a giant larva more than twice the weight of a normal adult. No good for propagating beetle genes, but a cornucopia for *Nosema* parasites. Giantism in beetle larvae is an extended phenotypic effect of protozoan genes.

And here is a case history to provoke even more Freudian anxiety than the Peter Pan beetles – parasitic castration! Crabs are parasitized by a creature called *Sacculina*. *Sacculina* is related to barnacles, though you would think, to look at it, that it was a parasitic plant. It drives an elaborate root system deep into the tissues of the unfortunate crab, and sucks nourishment from its body. It is probably no accident that among the first organs that it attacks are the crab's testicles or ovaries; it spares the organs that the crab needs to survive – as opposed to reproduce – till later. The crab is effectively castrated by the parasite. Like a fattened bullock, the castrated crab diverts energy and resources away from reproduction and into its own body – rich pickings for the parasite at the expense of the crab's reproduction. Very much the same story as I conjectured for *Nosema* in the flour beetle and for the fluke in the snail. In all these cases the changes in the host, if we accept that they are Darwinian adaptations for the benefit of the parasite, must be seen as

extended phenotypic effects of parasite genes. Genes, then, reach outside their 'own' body to influence phenotypes in other bodies. (242-243)

Wood-boring ambrosia beetles (of the species *Xyleborus ferrugineus*) are parasitized by bacteria that not only live in their host's body but also use the host's eggs as their transport into a new host. The genes of such parasites therefore stand to gain from almost exactly the same future as the genes of their host. The two sets of genes can be expected to 'pull together' for just the same reason as all the genes of one individual organism normally pull together. It is irrelevant that some of them happen to be 'beetle genes', while others happen to be 'bacterial genes'. Both sets of genes are 'interested' in beetle survival and the propagation of beetle eggs, because both 'see' beetle eggs as their passport to the future. So the bacterial genes share a common destiny with their host's genes, and in my interpretation we should expect the bacteria to cooperate with their beetles in all aspects of life. (243-244)

Our own genes cooperate with one another, not because they *are* our own but because they share the same outlet – sperm or egg – into the future. If any genes of an organism, such as a human, could discover a way of spreading themselves that did not depend on the conventional sperm or egg route, they would take it and be less cooperative. This is because they would stand to gain by different set of future outcomes from the other genes in the body. We've already seen examples of genes that bias meiosis in their own favour. Perhaps there are also genes that have broken out of the sperm/egg 'proper channels' altogether and pioneered a sideways route.

There are fragments of DNA that are not incorporated in chromosomes but float freely and multiply in the fluid contents of cells, especially bacterial cells. They go under various names such as viroids or plasmids. A plasmid is even smaller than a virus, and it normally consists of only a few genes. Some plasmids are capable of splicing themselves seamlessly into a chromosome. So smooth is the splice that you can't see the join: the plasmid is indistinguishable from any other part of the chromosome. The same plasmids can also cut themselves out again. This ability of DNA to cut and splice, to jump in and out of chromosomes at the drop of a hat, is one of the more exciting facts that have come to light since the first edition of this book was published. [...] From some points of view it does not really matter whether these fragments originated as invading parasites or breakaway rebels. Their likely behaviour will be the same. (245-246)

When we have a cold or a cough, we normally think of the symptoms as annoying byproducts of the virus's activities. But in some cases it seems more probable that they are deliberately engineered by the virus to help it to travel from one host to another. Not content with simply being breathed into the atmosphere, the virus makes us sneeze or cough explosively. The rabies virus is transmitted in saliva when one animal bites another. In dogs, one of the symptoms of the disease is that normally peaceful and friendly animals become ferocious biters, foaming at the mouth. Ominously too, instead of staying within a mile or so of home like normal dogs, they turn into restless wanderers, propagating the virus far afield. It has even been suggested that the well-known hydrophobic symptom encourages the dog to shake the wet foam from its mouth – and with it the virus. I do not know of any direct evidence that sexually transmitted diseases increase the libido of sufferers, but I conjecture that it would be worth looking into. Certainly at least one alleged aphrodisiac, Spanish Fly, is said to work by inducing an itch ... and make people itch is just the kind of thing viruses are good at. (246-247)

So enticing is the red gape of a cuckoo nestling that it is not uncommon for ornithologists to see a bird dropping food into the mouth of a baby cuckoo sitting in some other bird's nest! A bird may be flying home, carrying food for its own young. Suddenly, out of the corner of its eye, it sees the red super-gape of a young cuckoo, in the nest of a bird of some quite different species. It is diverted to the alien nest where it drops into the cuckoo's mouth the food that had been destined for its own young. The 'irresistibility theory' fits with the views of early German ornithologists who referred to foster-parents as behaving like 'addicts' and to the cuckoo nestling as their 'vice'. It is only fair to

add that this kind of language finds less favour with some modern experimenters. But there's no doubt that if we do assume that the cuckoo's gape is a powerful drug-like super-stimulus, it becomes very much easier to explain what is going on. It becomes easier to sympathize with the behaviour of the diminutive parent standing on the back of its monstrous child. It is not being stupid. 'Fooled' is the wrong word to use. Its nervous system is being controlled, as irresistibly as if it were a helpless drug addict, or as if the cuckoo were a scientist plugging electrodes into its brain. (249)

A bird cuckoo deposits her egg and disappears. Some ant cuckoo females make their presence felt in more dramatic fashion. I don't often give Latin names, but *Bothrimyrmex regicidus* and *B. decapitans* tell a story. These two species are both parasites on other species of ants. Among all ants, of course, the young are normally fed not by parents but by workers, so it is workers that any would-be cuckoo must fool or manipulate. A useful first step is to dispose of the worker's own mother with her propensity to produce competing brood. In these two species the parasite queen, all alone, steals into the nest of another ant species. She seeks out the host queen, and rides about on her back while she quietly performs, the quote Edward Wilson's artfully macabre understatement, 'the one act for which she is uniquely specialized: slowly cutting off the head of her victim'. The murderess is then adopted by the orphaned workers, who unsuspectingly tend her eggs and larvae. Some are nurtured into workers themselves, who gradually replace the original species in the nest. Others become queens who fly out to seek pastures new and royal heads yet unsevered.

But sawing off heads is a bit of a chore. Parasites are not accustomed to exerting themselves if they can coerce a stand-in. My favourite character in Wilson's *The Insect Societies* is *Monomorium santschii*. This species, over evolutionary time, has lost its worker caste altogether. The host workers do everything for their parasites, even the most terrible task of all. At the behest of the invading parasite queen, they actually perform the deed of murdering their own mother. The usurper doesn't need to use her jaws. She uses mind-control. How she does it is a mystery; she probably employs a chemical, for ant nervous systems are generally highly attuned to them. If her weapon is indeed chemical, then it is as insidious a drug as any known to science. For think what it accomplishes. It floods the brain of the worker ant, grabs the reins of her muscles, woos her from deeply ingrained duties and turns her against her own mother. For ants, matricide is an act of special genetic madness and formidable indeed must be the drug that drives them to do it. In the world of the extended phenotype, as not how an animal's behaviour benefits its genes; ask instead whose genes it is benefiting. It is hardly surprising that ants are exploited by parasites, not just other ants but an astonishing menagerie of specialist hangers-on. Worker ants sweep a rich flow of food from a wide catchment area into a central hoard which is a sitting target for freeloaders. Ants are also good agents of protection: they are well-armed and numerous. The aphids of Chapter 10 could be seen as paying out nectar to hire professional bodyguards. Several butterfly species live out their caterpillar stage inside an ants' nest. Some are straightforward pillagers. Others offer something to the ants in return for protection. Often they bristle, literally, with equipment for manipulating their protectors. The caterpillar of a butterfly called *Thisbe irenea* has a sound-producing organ in its head for summoning ants, and a pair of telescopic spouts near its rear end which exude seductive nectar. On its shoulders stands another pair of nozzles, which cast an altogether more subtle spell. Their secretion seems to be not food but a volatile potion that has a dramatic impact upon the ants' behaviour. An ant coming under the influence leaps clear into the air. Its jaws open wide and it turns aggressive, far more eager than usual to attack, bite and sting any moving object. Except, significantly, the caterpillar responsible for drugging it. Moreover, an ant under the sway of a dope-peddling caterpillar eventually enters a state called 'binding', in which it becomes inseparable from its caterpillar for a period of many days. Like an aphid, then, the caterpillar employs ants as bodyguards, but it goes one better. Whereas aphids rely on the ant's normal aggression against predators, the caterpillar administers an aggression-arousing drug and it seems to slip them something additively binding as well. (251-253)

[...] the Central Theorem of the Extended Phenotype: *An animal's behaviour tends to maximize the survival of the genes 'for' that behaviour, whether or not those genes happen to be in the body of the particular animal performing it.* (253)

The fundamental units of natural selection, the basic things that survive or fail to survive, that form lineages of identical copies with occasional random mutations, are called replicators. DNA molecules are replicators. They generally, for reasons that we shall come to, gang together into large communal survival machines or 'vehicles'. The vehicle that we know best are individual bodies like our own. A body, then, is not a replicator; it is a vehicle. I must emphasize this, since the point has been misunderstood. Vehicles don't replicate themselves; they work to propagate their replicators. Replicators don't behave, don't perceive the world, don't catch prey or run away from predators; they make vehicles that do all those things. For many purposes it is convenient for biologists to focus their attention at the level of the vehicle. For other purposes it is convenient for them to focus their attention at the level of the replicator. Gene and individual organism are not rivals for the same starring role in the Darwinian drama. They are cast in different, complementary and in many respects equally important roles, the role of replicator and the role of a vehicle. (254)

The essential quality that an entity needs, if it is to become an effective gene vehicle, is this. It must have an impartial exit channel into the future, for all the genes inside it. This is true of an individual wolf. The channel is the thin stream of sperms, or eggs, which it manufactures by meiosis. It is not true of the pack of wolves. Genes have something to gain from selfishly promoting the welfare of their own individual bodies, at the expense of other genes in the wolf pack. A bee-hive, when it swarms, appears to produce by broad-fronted budding, like a wolf pack. But if we look more carefully we find that, as far as the genes are concerned, their destiny is largely shared. The future of the genes in the swarm is, at least to a large extent, lodged in the ovaries of one queen. This is why [...] the bee colony looks and behaves like a truly integrated single vehicle. (256)

Why did genes gang up in cells? [...] DNA molecules make proteins. Proteins work as enzymes, catalysing particular chemical reactions. Often a single chemical reaction is not sufficient to synthesize a useful end-product. In a human pharmaceutical factory the synthesis of a useful chemical needs a production line. [...]

Nowadays this cooperation between genes goes on within cells. It must have started as rudimentary cooperation between self-replicating molecules in the primeval soup (or whatever primeval medium there was). Cell walls perhaps arose as a device to keep useful chemicals together and stop them leaking away. Many of the chemical reactions in the cell actually go on in the fabric of membranes; a membrane acts as a combined conveyor-belt and test-tube rack. But cooperation between genes did not stay limited to cellular biochemistry. Cells came together (or failed to separate after cell division) to form many-celled bodies.

This brings us to the second of my three questions. Why did cells gang together; why the lumbering robots? This is another question about cooperation. But the domain has shifted from the world of molecules to a larger scale. Many-celled bodies outgrow the microscope. They can even become elephants or whales. Being big is not necessarily a good thing: most organisms are bacteria and very few are elephants. But when the ways of making a living that are open to small organisms have all been filled, there are still prosperous livings to be made by larger organisms. Large organisms can eat smaller ones, for instance, and can avoid being eaten by them.

The advantages of being in a club of cells don't stop with size. The cells in the club can specialize, each thereby becoming more efficient at performing its particular task. Specialist cells serve other cells in the club and they also benefit from the efficiency of other specialists. If there are many cells, some can specialize as sensors to detect prey, others as nerves to pass on the message, others as stinging cells to paralyse the prey, muscle cells to move tentacles and catch the prey, secretory cells to dissolve it and yet others to absorb the juices. We are a clone. All contain the same genes, although different genes will be turned on in the different specialist cells.

Genes in each cell type are directly benefiting their own copies in the minority of cells specialized for reproduction, the cells of the immortal germ line.

So, to the third question. Why do bodies participate in a 'bottlenecked' life cycle?

To begin with, what do I mean by bottlenecked? No matter how many cells there may be in the body of an elephant, the elephant began life as a single cell, a fertilized egg. The fertilized egg is a narrow bottleneck with, during embryonic development, widens out into the trillions of cells of an adult elephant. And no matter how many cells, of no matter how many specialized types, cooperate to perform the unimaginably complicated task of running an adult elephant, the efforts of all those cells converge on the final goal of producing single cells again – sperms or eggs. The elephant not only has its beginning in a single cell, a fertilized egg. Its end, meaning its goal or end-product, is the production of single cells, fertilized eggs of the next generation. (257-259)

[There are] three reasons why a bottlenecked life history tends to foster the evolution of the organism as a discrete and unitary vehicle. These three may be labelled, respectively, 'back to the drawing board', 'orderly timing-cycle', and 'cellular uniformity'. Which came first, the bottlenecking of the life cycle, or the discrete organisms? I should like to think that they evolved together. Indeed I suspect that the essential, defining feature of an individual organism *is* that it is a unit that begins and ends with a single-celled bottleneck. If life cycles become bottlenecked, living material seems bound to become boxed into discrete, unitary organisms. And the more that living material is boxed into discrete survival machines, the more will the cells of those survival machines concentrate their efforts on that special class of cells that are destined to ferry their shared genes through the bottleneck into the next generation. The two phenomena, bottlenecked life cycles and discrete organisms, go hand in hand. As each evolves, it reinforces the other. The two are mutually enhancing, like the spiralling feelings of a woman and a man during the progress of a love affair. [...]

Let me end with a brief manifesto, a summary of the entire selfish gene/extended phenotype view of life. It is a view, I maintain, that applies to living things everywhere in the universe. The fundamental unit, the prime mover of all life, is the replicator. A replicator is anything in the universe of which copies are made. Replicators come into existence, in the first place, by chance, by the random jostling of smaller particles. Once a replicator has come into existence it is capable of generating an indefinitely large set of copies of itself. No copying process is perfect, however, and the population of replicators comes to include varieties that differ from one another. Some of these varieties turn out to have lost the power of self-replication, and their kind ceases to exist when they themselves cease to exist. Others can still replicate, but less efficiently. Yet other varieties happen to find themselves in possession of new tricks: they turn out to be even better self-replicators than their predecessors and contemporaries. It is their descendants that come to dominate the population. As time goes by, the world becomes filled with the most powerful and ingenious replicators.

Gradually, more and more elaborate ways of being a good replicator are discovered. Replicators survive, not only by virtue of their own intrinsic properties, but by virtue of their consequences on the world. These consequences can be quite indirect. All that is necessary is that eventually the consequences, however tortuous and indirect, feed back and affect the success of the replicator at getting itself copied.

The success that a replicator has in the world will depend on what kind of a world it is – the pre-existing conditions. Among the most important of these conditions will be the other replicators and their consequences. Like the English and German rowers, replicators that are mutually beneficial will come to predominate in each other's presence. At some point in the evolution of life on our earth, this ganging up of mutually compatible replicators began to be formalized in the creation of discrete vehicles – cells and, later, many-celled bodies. Vehicles that evolved a bottlenecked life cycle prospered, and became more discrete and vehicle-like.

This packaging of living material into discrete vehicles became such a salient and dominant feature that, when biologists arrived on the scene and started asking questions about life, their questions were mostly about vehicles – individual organisms. The individual organism came first in

the biologist's consciousness, while the replicators – now known as genes – were seen as part of the machinery used by individual organisms. It requires a deliberate mental effort to turn biology the right way up again, and remind ourselves that the replicators come first, in importance as well as in history.

One way to remind ourselves is to reflect that, even today, not all the phenotypic effects of a gene are bound up in the individual body in which it sits. Certainly in principle, and also in fact, the gene reaches out through the individual body wall and manipulates object in the world outside, some of them inanimate, some of them other living beings, some of them a long way away. With only a little imagination we can see the gene as sitting at the centre of a radiating web of extended phenotypic power. And an object in the world is the centre of a converging web of influence from many genes sitting in many organisms. The long reach of the gene knows no obvious boundaries. The whole world is criss-crossed with causal arrows joining genes to phenotypic effects, far and near.

It is an additional fact, too important in practice to be called incidental but not necessary enough in theory to be called inevitable, that these causal arrows have become bundled up. Replicators are no longer peppered freely through the sea; they are packaged in huge colonies – individual bodies. And phenotypic consequences, instead of being evenly distributed throughout the world, have in many cases congealed into those same bodies. But the individual body, so familiar to us on our planet, did not have to exist. The only kind of entity that has to exist in order for life to arise, anywhere in the universe, is the immoral replicator. (264-266)

#### *Endnotes to chapter 4.*

I said that an ordinary serial computer can create an illusion of being a parallel processor, by rotating its 'attention' sufficiently fast around a number of tasks. We could say that there is a *virtual* parallel processor sitting atop a serial hardware. Dennett's idea is that the human brain has done exactly the reverse. The hardware of the brain is fundamentally parallel, like that of the Edinburgh machine. And it runs software designed to create an illusion of serial processing: a serially processing virtual machine riding on top of a parallel architecture. The salient feature of the subjective experience of thinking, Dennett thinks, is the serial 'one-thing-after-another', 'Joycean', stream of consciousness. He believes that most animals lack this serial experience, and use brains directly in their native, parallel-processing mode. Doubtless the human brain, too, uses its parallel architecture directly for many of the routine tasks of keeping a complicated survival machine ticking over. But, in addition, the human brain evolved a software virtual machine to simulate the illusion of a serial processor. The mind, with its serial stream of consciousness, is a virtual machine, a 'user-friendly' way of experiencing the brain, just as the 'Macintosh User Interface' is a user-friendly way of experiencing the physical computer inside its grey box.

It is not obvious why we humans needed a serial virtual machine, when other species seem quite happy with their unadorned parallel machines. Perhaps there is something fundamentally serial about the more difficult tasks that a wild human is called upon to do, or perhaps Dennett is wrong to single us out. He further believes that the development of the serial software has been a largely cultural phenomenon, and again it is not obvious to me why this should be particularly likely. But I should add that, at the time of my writing, Dennett's paper is unpublished and my account is based on recollections of his 1988 Jacobsen Lecture in London. The reader is advised to consult Dennett's own account when it is published, rather than rely on my doubtless imperfect and impressionistic – maybe even embellished – one.

The psychologist Nicholas Humphrey, too, has developed a tempting hypothesis of how the evolution of a capacity to simulate might have led to consciousness. In his book, *The Inner Eye*, Humphrey makes a convincing case that highly social animals like us and chimpanzees have to become expert psychologists. Brains have to juggle with, and simulate, many aspects of the world. But most aspects of the world are pretty simple in comparison to brains themselves. A social animal lives in a world of others, as world of potential mates, rivals, partners, and enemies. To survive and prosper in such a world, you have to become good at predicting what these other individuals are going to do next. Predicting what is going to happen in the inanimate world is a

piece of cake compared with predicting what is going to happen in the social world. Academic psychologists, working scientifically, aren't really very good at predicting human behaviour. Social companions, using minute movements of the facial muscles and other subtle cues, are often astonishingly good at reading minds and second-guessing behaviour. Humphrey believes that this 'natural psychological' skill has become highly evolved in social animals, almost like an extra eye or other complicated organ. The 'inner eye' is the evolved social-psychological organ, just as the outer eye is the visual organ. (279-281)

*Endnotes to chapter 5.*

Digger wasps are not the familiar social wasps of our autumn jam-pots, which are neuter females working for a colony. Each female digger wasp is on her own, and she devotes her life to providing shelter and food for a succession of her larvae. Typically, a female begins by digging a long bore-hole into the earth, at the bottom of which is a hollowed-out chamber. She then sets off to hunt prey (katydids or longhorned grasshoppers in the case of the great golden digger wasp). When she finds one she stings it to paralyse it, and drags it back into her burrow. Having accumulated four or five katydids she lays an egg on the top of the pile and seals up the burrow. The egg hatches into a larva, which feeds on the katydids. The point about the prey being paralysed rather than killed, by the way, is that they don't decay but are eaten alive and are therefore fresh. It was this macabre habit, in the related Ichneumon wasp, that provoked Darwin to write: 'I cannot persuade myself that a beneficent and omnipotent God would have designedly created the Ichneumonidae with the express intention of their feeding within the living bodies of Caterpillars ...' He might as well have used the example of a French chef boiling lobsters alive to preserve the flavour. Returning to the life of the female digger wasp, it is a solitary one except that other females are working independently in the same area, and sometimes they occupy one another's burrows rather than go to the trouble of digging a new one. (284)

*Endnotes to chapter 9.*

An erect human penis can be so hard and stiff that people jokingly express scepticism that there is no bone inside. As a matter of fact lots of mammals do have a stiffening bone, the baculum or os penis, to help the erection along. What's more, it is common among our relatives the primates; even our closest cousin the chimpanzee has one, although admittedly a very tiny one which may be on its evolutionary way out. There seems to have been a tendency to reduce the os penis in the primates; our species, along with a couple of monkey species, has lost it completely. So, we have got rid of the bone that in our ancestors presumably made it easy to have a nice stiff penis. Instead, we rely entirely on a hydraulic pumping system, which one cannot but feel is a costly and roundabout way of doing things. And, notoriously, erection can fail – unfortunate, to say the least, for the genetic success of a male in the wild. What is the obvious remedy? A bone in the penis, of course. So why don't we evolve one? For once, biologists of the 'genetic constraints' brigade cannot cop out with 'Oh, the necessary variation just couldn't arise.' Until recently our ancestors had precisely such a bone and we have actually gone out of our way to lose it! Why? (307)