

# 1 DARWIN'S ARGUMENT AND THREE PROBLEMS: HERITABILITY, SEXUAL SELECTION AND ALTRUISM

Some of the questions addressed in this chapter

- What is natural selection?
- What problems did the theory of natural selection face after Darwin's death?
- How were the problems addressed?
- What are the laws of inheritance?
- What is sexual selection theory?
- How can we account for altruistic behaviour according to natural selection?

## SOME KEY TERMS AND CONCEPTS

Adaptation; Altruism; Chromosomes; Darwinism; Fitness; Function; Genes; Heritability; Lamarck(ism); Mendel(ian); Natural selection; Reproductive success; Sexual selection; Variation.

## LEARNING OBJECTIVES

Having studied this chapter you should be better able to:

- Outline the theory of natural selection.
- Indicate which parts of the process Darwin did not fully understand.
- Outline the mechanisms which underlie evolution.

## INTRODUCTION

In this chapter we will look at Darwin's argument for the theory of natural selection and its logic. We will see that it is a good theory in that it offers a parsimonious account of the fact that animal and plant species are typically well designed to survive and reproduce in

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the environments in which they occur. Soon after its presentation, Darwin's theory gained currency in the scientific community and was widely accepted as a plausible account of how species come about and evolve over time. However, it still faced a number of problems. It wasn't entirely clear how characteristics of parents were passed to offspring, why some characteristics seemingly detrimental to long-term survival persisted in various species and why all organisms were not relentlessly selfish. These problems were tackled in time and we will briefly review the solutions.

### DARWIN'S ARGUMENT

#### BOX 1.1 ARE YOU A DARWINIAN? BEFORE WE BEGIN, ASK YOURSELF:

'Are you a Darwinian?'

Do you believe that humans have evolved?

Do you accept that that you are the product of evolution?

Do you believe that humans are adapted?

Do you accept that you are fitted to, or designed to survive in, certain specific environments?

Do you believe that what we are adapted to and for can be addressed by our natural history?

Do you believe that the physical form that you take is explicable in terms of past selection pressures?

I suggest that if you either do or are inclined to say 'yes' to these question then you are indeed a Darwinian.

Charles Darwin's argument for the natural selection of evolved life forms is not complicated and is based on observations. As was suggested soon after the publication of his *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (Darwin, 1859), Darwin's interpretation of his evidence appears, on hindsight, to be obvious. The theory of natural selection can be presented as comprising three basic premises: the variation premise, the heritability premise and the adaptation premise. Together these premises led Darwin to the conclusion that life forms on earth evolved by a blind process he called natural selection. Let us look at the premises a little more closely.

### VARIATION

The **variation** premise is based upon the observation that organisms within a species differ in their physical and behavioural characteristics. Following the conventions of common language, Darwin called identifiable differences between individuals of the same species 'variations'. Variation is demonstrated by the fact that no two instances of a species are physically (save the possibility of monozygotic siblings, more commonly called or 'identical twins') or behaviourally identical.

## INHERITANCE

The **inheritance** premise is based on the observation that variations between members of a species are frequently transmitted from parent to progeny. This is simply to say that identifiable characteristics of individual organisms are passed on to their offspring such that the offspring are distinct from other by virtue of the characteristics. This observation allows us to say that, *ceteris paribus* (all things being equal), offspring will resemble their progenitors more than they will any other randomly selected member of the species population.

## ADAPTATION

The **adaptation** premise is based on the observation that organisms are 'fitted' to their environments. To say an organism is fitted to its environment is to say that in the wild (as opposed to in a zoo or a laboratory) it exhibits physical and behavioural characteristics which enable it to cope with and exploit features of the environment in which it lives. These features Darwin called 'adaptations'.

## DARWIN'S CONCLUSION

Having established that organisms vary, that the variations can be inherited, and that species were adapted to the environments in which they are naturally found, Darwin inferred that not all variations are 'equal'. What he meant by saying they are not equal is that not all individual differences fitted the carrier equally well to the environment and the problem of reproduction. Darwin argued that as a result of variations some members of a species not only survived longer than others but, crucially, some produced more offspring than others. Invoking the observable fact that variations are heritable, Darwin concluded that variations which facilitate survival and reproduction will be more numerous in the next and future generations than others. The continual and inevitable reiteration of the process wherein some members of a species reproduce and pass on the characteristics which enabled them to survive and reproduce is what we call natural selection. The iteration of this process shapes and reshapes a species over time. Such shaping and reshaping is what we call evolution.

## DARWIN'S PROBLEMS

As straightforward as it appeared to those of his contemporaries such as Thomas Huxley who proselytised on Darwin's behalf, Darwin himself and critics within the scientific community identified problems with his theory of evolution by natural selection. One of the problems concerned the observable fact that many typical features of different species appeared to hinder rather than help them to survive. The male peacock's tail is, perhaps, the most salient and oft-given example. Its size and visibility make it expensive to produce in metabolic terms and renders the bird vulnerable to predators. We will call this the

‘problem of non-fitness’. Darwin solved the problem himself in his volume *The Descent of Man, and, Selection in Relation to Sex* (Darwin, 1871) with his theory of **sexual selection** but his solution was not widely accepted until the 1930s. A second problem was the mechanism of inheritance. Darwin accepted that he did not know how it was that adaptive variations were transmitted from parent to offspring. He also did not know that the mechanism and rules of inheritance had, to a considerable extent, been discovered by Gregor Mendel. And a third problem, and one that Darwin said made him feel ‘sick’, was that of **altruism**. According to the theory, organisms should behave purely in their own self-interest but innumerable observations suggested that this ‘rule’ was routinely broken by any number of different species. The solution to the problem of altruism was presented in the 1960s by William Hamilton. The problem of altruism was solved by seeing the correct level at which natural selection operates – the genetic level. Let us now look at the solutions to the problems of non-fitness, heritability and altruism in turn. What we learn here will be essential to our understanding of later analyses of the evolutionary basis of human thought and behaviour.

## THE PROBLEM OF NON-FITNESS AND SEXUAL SELECTION THEORY

As we have noted, many organisms, including humans, exhibit physical and behavioural characteristics that are typical of the species but appear to be detrimental to the bearer’s prospects of survival and longevity. An example that we will examine in more detail in Chapter 8 ‘Competition, aggression and violence’ is what has been called the ‘**young male syndrome**’ – the apparently unnecessarily risky, and often life-threatening, behaviour exhibited by post-pubescent human males (Wilson and Daly, 1997). Being typical of a species any such characteristics are, according to theory, evolved and therefore, naturally selected. But, if the characteristics mitigate against survival and longevity how could they be repeatedly selected for and why would they persist?

In *The Descent of Man and Selection in Relation to Sex* Darwin reinforced his argument that evolution does not favour longevity *per se*, but it favours reproductive success. Now, whilst any given organism has to survive for some period of time – a minimum enough time to reach reproductive maturity – its reproductive success determines how many of its characteristics will be represented in the next generation rather than its life span. Of course, there is a relationship between the two given that longevity is likely to aid reproductive success. However, the maxim ‘Don’t count the candles on the cake, count the kiddies’ holds. What we now call **Darwinian fitness** – the long-term survival over evolutionary time of any given heritable characteristics – is determined by the reproductive success of its bearer and not the length of its life. In the currency of natural selection it is of no use if an organism lives very much longer than other members of her or his species if he or she does not reproduce.

With this insight in mind let us now outline **sexual selection** theory. Sexual selection theory argues that physical and behavioural traits that mitigate against longevity – that

is, carry a cost to the bearer with regard to life overall life expectancy – but facilitate reproduction – that is, aid the bearer in attracting mates and parenting viable offspring – can persist in a population overtime. Let us return to the peacock's tail for an example. Whilst the large and elaborate plumage of the male bird is costly to grow and makes the animal vulnerable to potential predators it also makes it visible and attractive to pea hens. In the case of peacocks the trade-off between the cost to longevity and the gain for reproductive success have favoured the elaborate tail which characterises the birds we see today. In short, sexual selection theory argues that the existence of variable heritable traits which seem to be useless or disadvantageous to survival can be explained if it can be shown that they confer an advantage with respect to reproductive success.

Sexual selection and natural selection are not necessarily mutually exclusive. A trait that enables an organism to enjoy reproductive success may also enable it to live longer. For example, better than average eye sight may enable an organism to spot predators, prey *and* this ability might make that organism more appealing to members of the opposite sex. However, to be confident that a given trait has evolved by sexual selection an analysis of its function should show that the trait is neutral or detrimental with regard to longevity and that it clearly facilitates reproductive success.

This is the reasoning behind the solution to the apparent problem of non-fitness. When we see that success over evolutionary time is determined by reproduction rather than survival we can also see that physical and behavioural characteristics which appear non-fit in survival terms may be fitness enhancing in reproductive terms.

As has been suggested, Darwin's proposal was not readily accepted when first introduced and it was further undermined by its rejection by the co-founder of evolutionary theory, Alfred Wallace (1823–1913). We might suppose that the emphasis on sex in the natural history of humans, and Darwin's emphasis on how the choices and preferences of females shape the evolution of most mammalian species including humans, was not well received in the late nineteenth century due to the sensitivities of the time. Sir Ronald Fisher (1890–1962) is, perhaps, most responsible for putting sexual selection at the centre of the theory of evolution and giving it nuance. His *The Genetical Theory of Natural Selection* (Fisher, 1930) proposed what has come to be known as '**run away selection**' (also occasionally referred to as 'Fisherian selection'). Based on sexual selection theory, run away selection theory further explicates how non-fit characteristic can come about, evolve and become species typical. It explains how sexual selection can accelerate the evolution of characteristics beyond that which would be possible via natural selection by supposing that once a preference for a trait (often a female preference for a trait in males) becomes established only those males showing extreme forms of the trait get to reproduce. The only limiting factor on the evolution of the trait is its metabolic cost and/or negative impact on longevity.

We will be revisiting, expanding upon, elaborating the theory of and examining research inspired by sexual selection theory in a number of subsequent chapters, especially Chapter 7 'Mate Selection, Chapter 8 'Competition, aggression and violence' and Chapter 11 'Evolution and language'.

## THE PROBLEM OF HERITABILITY

### BOX 1.2 THE DIFFERENCE BETWEEN PROCESSES AND MECHANISMS: TRY IT THIS WAY ...

#### Darwin and Mendel:

As has been pointed out (Plotkin, 2002) Darwin explained the **process** by which change came about over time but he was unable to explain the **mechanisms** which embodied the process. To understand the distinction between process and mechanism consider the difference between the set of rules which govern how your essays or research reports are assessed and the actual work that is done – reading, appraising, commenting – in order to assess them to. The rules provide an abstract description of the process that has to be gone through. The appraisal is the observable mechanism that instantiates the rules. Contemporary evolutionary theory is a synthesis – a marrying together – of the process that Darwin described and the mechanisms that Mendel and his successors have described.

Darwin was not the first to suggest that variations exhibited by individuals of a species are heritable and he was not the first to propose a theory of evolution. Probably the most influential of his predecessors was the French thinker and scientist Jean-Baptiste Lamarck (1744–1829). Lamarck's theory of evolution was presented in a book whose English translation is *Zoological Philosophy: Exposition with Regard to the Natural History of Animals* published in 1809 (Richards, 1987) Lamarck proposed that evolution comes about via a process of **inheritance of acquired characteristics** – an idea also known as **Lamarckism**. The idea is that parents (of whatever species) pass on changes that have occurred in their physical make-up during the course of their existence to their offspring. Here we can appeal to another well-worn but illustrative example – that of the blacksmith who acquires larger than ordinary arm muscles and then passes on these acquired characteristics to his sons. Despite Lamarck's failure to offer evidence in its favour it persisted through the nineteenth century and retains a certain appeal to this day. Why was this so?

There are at least three reasons. First, it was the first forcefully articulated theory of evolution by a respected naturalist in an age wherein the developing scientific community was amenable to the general idea that life had come about and evolved courtesy of forces other than the divine intervention of a god-like being. Second, when applied to humans the idea of acquired characteristics suggested that evolution when thought of as 'improvement' was possible in response to human striving. And, third, when seen as the accumulation of useful knowledge and functional traditions, social and cultural evolution appears to fit the term 'acquisition of characteristics'. In the rapidly changing Europe of the late eighteenth and early nineteenth centuries it seemed to make sense to say that the hard-won characteristics that defined certain persons and social classes were bequeathed to their children, i.e. that the diligence, thrift, educational and moral outlook acquired by the expanding middle classes in newly industrialised European cities would be handed down to and exhibited by



**Figure 1.1** Jean-Baptiste Lamarck

their children. In the absence of a plausible mechanism what would accommodate the transmission of heritable characteristics over multiple generations, through successive editions of the *Origin* Darwin drifted towards a Lamarckian position towards the end of his life (Badcock, 1994). Today Lamarck's theory is seen to be an inadequate account of change through time because the selection courtesy of use or disuse is not sophisticated enough to accommodate the innumerable very finely grained adaptations that comprised even simple organisms.

Unbeknown to Darwin, the problem of inheritance had, in essence, already been solved. In 1865 Gregor Mendel (1822–1884) presented his research to the Natural History Society of Brunn – Brunn being a town in Bavaria, Germany. Mendel published his findings a year later in the Society's journal. Mendel's idea was that organisms are composed of more-or-less discrete and fixed characteristics in much the same way that any machine is. What have come to be known as 'Mendel's Laws' can be derived from the evidence he accumulated. We will briefly consider the 'Laws' before moving on to see how Mendelian genetics solves Darwin's problem of heritability.

## LAW OF SEGREGATION

An organism which reproduces via sexual reproduction transmits unchanged to its sex cells (or **gamete**) one of two set of instructions it carries for any given discrete characteristic. Sex cells in humans are male sperm and female ova. Also called 'factors' or 'traits' these instructions are what we call genes. Reproduction involves the passing on of some of these fixed characteristics to their offspring via sex cells. Whilst he did not use the term 'gene' (it was introduced by Wilhelm Johannsen in 1909), Mendel claimed that the sex cells from the

two parents carried very specific instructions concerning the characteristics that the new offspring would exhibit. From a Darwinian point of view the key point is that the inherited factors or traits are passed on unchanged. What this means is that the offspring may look like a 'blend' of the parents – like a cocktail of blue and yellow paints producing green – but in actuality it is a recombination of fixed characteristics. The new mixture looks green but on closer examination we see that it is still made up of blue components and yellow components. Part of the uniqueness of the new individual comes not from blending characteristics but from but from a recombination of particular characteristics.

## LAW OF INDEPENDENT ASSORTMENT

Applying to both prospective parents, the factors or traits are randomly assigned to any given sex cell – sperm or ovum. Look at Table 1.1 'Law of Independent Assortment. We can think of what happens with independent assortment by imagining that the pairs of letters underneath 'Pop's Genome' represents all of his genes. The capitalised letters represent one variant of the gene, and the lower-case letters represent another. Let us say that the 'a's' represent one part or feature of Pop, the 'b's' another and so on. The same goes for 'Ma's Genome'. Independent assortment refers to the process whereupon when Pop produces a sex cell (a sperm in humans) a random selection of one of each type of gene goes into the sex cell. In the example shown it is a **B c D e**, but it could be **ABCDE** or **abcde**, or any other combination. Again, the same applies to Ma's sex cell. These two cells then combine to produce the new genotype.

**Table 1.1 Law of Independent Assortment**

Pop's Genome	Ma's Genome	Baby's Genome
Aa	aA	aA
Bb	bB	<b>Bb</b>
Cc	cC	cC
Dd	dD	<b>Dd</b>
Ee	eE	eE
Sperm – a <b>B c D e</b>		Egg – A <b>b C d E</b>

The importance of the Law of Independent Assortment for Darwinism comes in its ability to explain how offspring vary from the parents and all other members of the species (save a monozygotic twin) when looked at as a whole whilst retaining discrete and unchanged traits from parents.

Before moving on to look at the Law of Dominance we will pause here to introduce a little more formal terminology. The variety of forms a factor or trait can take is called an **allele**. For the 'alpha' factor or trait in the imaginary example above possible alleles are **A**, **A**, **a** and **a**. There could be many others in the population such as **A A a** and **a**. Each one



codes for a specific characteristic of the organism such as hair or eye colour, size of a particular anatomical structure or the physiology of a structure. The set of alleles which a new individual organism ends up is called its **genotype**. It is the genotype – the collection of alleles – which codes for and builds the mature organism which is also known as the **phenotype**.

## LAW OF DOMINANCE

As we can see from the illustration in Box 1.3, alleles are paired and offspring receive one version of each from each parent. However, only one gene gets expressed. This means that only one is 'turned on' and codes for the particular characteristic. That which is expressed is called the **dominant gene**. That which is not expressed is called the **recessive gene**. We should note that the terms 'dominant' and 'recessive' do not mean and should not be taken to imply 'better' or 'worse'. They mean only expressed or not expressed, activated or not-activated.

The important point about dominant and recessive genes from a Darwinian perspective is that they demonstrate that a preponderance of observable expressed characteristics in a population of organisms can hide the fact that an equal number of genes coding for a different variation of the trait exist in a population and that the expression of recessive genes (often after many generations) shows that traits cannot be 'blended' out of existence.

To recap, Mendel's Laws, based on the notion that fixed and particular characteristics are inherited from parents via sex cells, show how variations could persist unchanged in organisms which, taken as a whole, appeared to be unique. However, Mendel's finding also raised a further problem for Darwinism. Given the seemingly fixed and permanent properties of genes, how do we account for evolutionary change in species as opposed to endless variations of the same basic template or design? The answer comes in the form of genetic mutations and the fact that the genes passed from parent to offspring are not always absolutely identical.

## MUTATION

**Mutation** refers to the imperfect replication of a gene. A mutated gene is an inexact copy of that held by a parent which ends up in a gamete and, subsequently, in a new genome. See Table 1.2 for an illustration.

Here we have the same schematic as in Table 1.1. The difference in detail can be seen in the genes in Pop's sperm and Ma's egg. Whilst Pop is carrying a B c D and e he donates *a* B c D *e* because a and e have mutated to *a* and *e*. Similarly, whilst Ma is carrying A b C d E she donates A b C d E because C has mutated to *C*. The outcome is an offspring which is not a collection of genes identical to those which reside in its parents. On the assumption that these mutations are novel (and let us do so for the sake of the illustration), what we have here is not simply an organism which is a variation on an established template or design but a new form of the species.

**Table 1.2 Mutations**

Pop's Genome	Ma's Genome	Baby Genome
Aa	aA	aA
Bb	bB	<b>Bb</b>
Cc	cC	cC
Dd	dD	<b>Dd</b>
Ee	eE	eE

Sperm – *a B c D e* Egg – *A b C d E*

Where the italicised letters refer to mutated genes, and upper-case letters refer to dominant genes.

Notice that only dominant genes get expressed and thus only one of the three mutations in the new genome in this case would be expressed

For our purposes there are three things to note about genetic mutations. One, the evidence suggests that they are rare and genes copy from donor to gamete with fidelity almost all of the time. Two, mutations are normally deleterious to the carrier – expressed mutations very rarely ‘improve’ the final phenotype in terms of its Darwinian fitness. And three, mutations – errors in the copying mechanism of genes – are the driving force in evolution. The rare mutations that do improve the fitness of the final phenotype which they code for can out-replicate alternative alleles with the result that over very many generations a species can evolve into something different.

Mendel’s discoveries allowed Darwinism to replace Lamarckism as the favoured theory of evolution because the idea that the inheritance of naturally selected particulate characteristics replaced the inheritance of acquired characteristics. Mendel also provided a scientifically well-attested means by which inheritance took place, it allowed evolution to be ‘natural’ or blind rather than purposive or teleological, and it provided a mechanism for variation and change that was slow, random and sex linked just as Darwin had proposed.

## THE PROBLEM OF ALTRUISM

A third problem for Darwin concerned the apparent lack of selfishness exhibited by many of the species he observed. To understand the problem it is useful to look at one of the key notions which had influenced Darwin.

Before formulating the theory of natural selection in the 1840s Darwin had read Thomas Robert Malthus’ (1766–1834) *An Essay on the Principle of Population* which was first published in 1798. Malthus’ *Essay* is, essentially, a political treatise concerned with population growth. Population growth was a topic of great interest in eighteenth-century Britain where it had quadrupled in less than 100 years (Woods, 1995). Of particular interest to Darwin was Malthus’ assertion that food supply can only grow at an arithmetic rate whilst population grows at a geometric rate: i.e. that agricultural advances can only increase food supply incrementally by fractions but population can grow by multiples.



**Figure 1.2** Thomas Robert Malthus

The general message that Darwin gleaned from Malthus was that population growth for any species is constrained by resources and the constraint is omnipresent. The arithmetic warranted the conclusion that the capacity for reproduction will always outstrip the resources required to sustain the resultant population. To be successful in such circumstances it seemed to follow that organisms cannot not compete with one another for the resources which sustain life. Accordingly, ever-persistent resource shortages allied to the necessity of competition for the limited resources implies that organisms should be profoundly selfish. According to natural selection, if an organism sacrificed itself or any resource needed for survival and reproduction (and this could be time and space as well as nutrients) to the benefit of another then that proclivity would, axiomatically, not be passed on to others. The conclusion seemed obvious: over evolutionary time selfishness will out-compete and eradicate selflessness.

However, Darwin saw it himself and the evidence from observations of various species in their natural settings contradicted the selfish selection formulation of natural selection. **Altruism** and apparent co-operation amongst species as diverse as ants, birds and primates offered what seemed to be sound reasons for believing that many individual organisms behaved in such a way as to promote the survival of the species to which they belonged. These observations and this thinking gave rise to **group selection** – the idea that members of a species acted for the good of the species.

It is not too difficult to see why group selection has an appeal over and above the evidence which gives it licence. It takes some of the ‘tooth and claw’ out of an evolutionary view of the natural world. With humans in mind, group selection seemed to offer grounds for optimism. Perhaps the highpoint of the group selection theory came with Wynn-Edwards’ volume *Animal Dispersion in Relation to Social Behaviour* (1962).

There are a number of conceptual and empirical problems with group selection theory and we will be examining some of them as well as looking at further reasons why the idea was, and remains, popular in Chapter 5 ‘Cooperation and Interdependence’. Now we will look at William Hamilton’s solution to the apparent conundrum of altruistic behaviour and one of the most important ideas in contemporary evolutionary theory – **kin selection** theory (also known as **inclusive fitness** theory).

## KIN SELECTION THEORY

Recall from our discussion of Mendelian inheritance that parents pass on to their offspring, and that which persists over time, are genes – instructions for particular and discrete characteristics. It is always tempting to think of natural selection as something that operates at the level of the individual – that it is you, me, Tom, Dick or Harriet that gets selected for or against. However, we need to remember that natural selection operates at the level of the gene. Why? Because natural selection works imperceptibly slowly, its winnowing process sifting characteristics favouring reproductive success through innumerable generations, it couldn’t work at the individual level simply because individuals do not persist long enough, and, because we do not clone ourselves, we don’t reproduce ourselves. But our genes do persist, replicate and clone. However, if we accept that the unit of selection is the gene, the following reformulation of the problem of altruism presents itself: how can one explain the existence of a gene that aids the reproduction of other genes?

As with much in evolutionary theory the answer may seem obvious when presented. And the answer, presented by William Hamilton (1936–2000) in two papers in the mid-1960s (Hamilton, 1964a, 1964b), rests on the observation that any given gene is selfish but not necessarily unique. Identical alleles are expected to be extant in a number of individuals. Furthermore, where there are multiple copies of genes, given the Mendelian rules of inheritance, the proximity of exact copies are likely to be found most frequently in families or kin-groups. With this in mind, we can see that a gene that motivates the phenotype it helps to build to help other phenotypes which carry a copy of itself assists in its own replication, and vice versa. The conclusion is that natural selection could favour acts of altruistic helping on the condition that the helper is genetically related to the person helped. Should you and the person next to you share half your genes in common then any reproductive success that they enjoy amounts to reproductive success for you when looked at from the genetic level of analysis.

### BOX 1.3 FORMULA FOR KIN SELECTION

Kin selection is formalisation as follows:

$B > C$

Where **B** = benefit to the reproductive success of the actor

Where **C** = cost to the actor in terms of its own reproductive success

Where **r** = the degree of relatedness between the benefactor and the benfittee.

In ordinary language it means that altruistic acts of helping can pay off for the helper provided the cost incurred is not greater than the benefit received by the related individual. To illustrate, it will pay Tom to help his sister Harriet if the help to her is worth more in terms of her final reproductive success than twice the cost to him in terms of his final reproductive success given that, all things being equal, they share half their genes in common courtesy of common descent. To reiterate courtesy of a parent-child scenario, it will pay Thomasina to help her child Dick if the help facilitates his reproductive success to more than twice the extent that it inhibits hers given that they share half their genes in common courtesy of common descent. The general point is that provided there is some degree of relatedness, there is always some potential that it will benefit the actor to jeopardise her own reproductive success provided the success of the other is enhanced.

Given that species with much smaller central nervous systems and far less elaborate cognitive abilities than humans appear to operate according to its edict it is supposed that, psychologically, all that is required for kin altruism to work is that an individual is able to identify others that carry the clone. This could be a simple counterfactual rule such as '*If raised with X then help*', or we need only invoke some sort of proximity calculation/rule such as '*Help those who look/smell like others around you*'. It is not necessary to suppose that either we or other species formally calculate who is and who is not related to us and to what degree we share which genes in common (Dawkins, 1976). The rough-and-ready way in which we calculate degrees of genetic relatedness has important implications. It may allow for what we might call 'virtual kin altruism' wherein we treat as kin others who we come to know well. We will look at the notion of virtual kin altruism in more detail in Chapter 4 'Cooperation and Interdependence'.

Hamilton's solution to the problem of altruism has four-fold appeal to Darwinism. First, the problem of how altruism could exist dissolves. Second, it is solved by invoking the same unit and level of selection as the unit of inheritance and the source of variation – the gene. Third, seeing the individual as potentially altruistic but the gene as selfish accommodates the selfish logic insisted on by Darwin. A fourth way in which Hamilton's solution adds weight to Darwinism comes in the way it facilitated analysis of seemingly altruistic acts between non-kin. Kin altruism enables us to see how pro-social, cooperative, interdependent behaviour can come about and become common in a whole population of organisms (Maynard-Smith, 1982). We will conclude this chapter with an overview of Robert Trivers' theory of reciprocal altruism.

## RECIPROCAL ALTRUISM

Further consideration of Hamilton's ideas suggests to us that altruism among kin is something of an illusion. The care provided by a parent to its child may look like it is unconditional, but from the gene-eye view, the parent is merely helping itself, aiding its own Darwinian fitness. We can see apparently unconditional assistance extended to brothers and sisters, cousins and grandchildren in a similar way. Trivers' account of how Darwin's theory can accommodate assistance given to unrelated others – **reciprocal altruism** theory – also invites some confusion because of the terminology used (Trivers, 1971). *Prima facie*, 'altruism' implies a one-way, unconditional act of giving whereas 'reciprocal' implies a

two-way conditional exchange. It is the second notion which is at the heart of Trivers' idea. Strictly, perhaps, we ought not use the term 'altruism' because reciprocal altruism theory claims that exchanges of favour can become common amongst members of a species (and, indeed, between species) provided favours are reliably and consistently repaid. According to Trivers and others reciprocal altruism – or what we might also call mutual assistance – can and has evolved to be a typical characteristic of many species, including humans, because it pays those who engage in it in terms of their reproductive success. It is especially apt to work well in species wherein the assistance of others can enable an organism to achieve a goal that would be either difficult or impossible to achieve alone. For example, it is easier to get another to scratch your back than it is to do it your self, and vice versa. Sexual reproduction itself is an example wherein the goal cannot be achieved with some sort of cooperation from another party, and there are many others. In Dennett's words, reciprocal altruism is a 'good trick', a mutually beneficial, cost-effective way of gaining desirable pay-offs (Dennett, 1995). In fact, so good a trick is mutual assistance that it can be a positive disadvantage not to engage in it, or to dodge debts if the consequence is a withdrawal of aid.

As we shall see when we explore the mechanics, arithmetic and psychology of kin selection and reciprocal altruism in further detail in Chapter 4 'Cooperation and interdependence', the claim that apparently altruistic acts are underpinned by genetic gain does not mean that an act of giving between kin does not feel like an expression and outcome of unconditional love, or that favours exchanged between acquaintances are not also expressions of care and affection. Evolutionary psychologists argue that evolution has shaped us to feel and think in ways which mask the biological functions being served. Whilst the functions served are real so too are the psychological states that serve them (Trivers, 1983).

## SUMMARY OF CHAPTER 1

Darwin's theory of evolution by natural selection rests on three observations. The first is that members of a species vary. The second is that offspring inherit characteristics from their parents. And the third is that species are adapted to their natural environments. From these observations Darwin concluded the accumulation of inherited variations that better fitted some organisms to solve the problem of survival and reproduction resulted in change in the species over time.

The emphasis on the need to reproduce allowed Darwin to explain why some characteristics of species seemed to be an impediment to their chances of surviving. What we have called the 'problem of non-fitness' is solved when we see that the overarching problem is not survival but reproduction and some characteristics persist because they assist reproduction at the cost of longevity.

However, Darwin did not know how inheritance worked, or why selfless behaviour was so common place. The solutions to the problem of inheritance and the problem of altruism were lay in the concept of the gene. Mendel's work led to the identification of genes as the mechanism by which inheritance works, and the work of Hamilton showed that because genes clone themselves they can code for organisms that assist others to their own

benefit. The result was kin selection theory and it provides the rationale behind the notion of the selfish gene. Trivers applied similar cost–benefit thinking to the issue of mutual self-assistance. His theory of reciprocal altruism explains how non-related members of a species can come to cooperate with one another.

## FURTHER READING

Apart from the references in this chapter you may find it interesting and useful to consult one or more of the following:

- Cronin, H. (1991) *The Ant and the Peacock*. Cambridge: Cambridge University Press – see Chapter 2 'A world without Darwin'.
- Fisher, R.A. (1997/orig. 1930) The nature of adaptation. In Ridley, M. (ed.) *Evolution*. Oxford: Oxford University Press – see pp. 112–115.
- Hume, D. (1997/orig. 1751) The argument from design. In Ridley, M. (ed.) *Evolution*. Oxford: Oxford University Press – see pp. 387–389.
- Huxley, T.H. (1894) *Man's Place in Nature and Other Essays*. London: Macmillan and Co. – see Chapter XIV 'The Darwinian Hypothesis'.
- Williams, G.C. (1997/orig. 1966) Adaptation and natural selection. In Ridley, M. (ed.) *Evolution*. Oxford: Oxford University Press – see pp. 115–118.