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THE EVOLUTION OF HUMAN ALTRUISM TOWARDS NON-KIN THROUGH SEXUAL SELECTION

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ABSTRACT

Altruistic or selfless behaviour is a major puzzle for evolutionary biology which predicts competition between organisms in the ‘struggle for existence’. One explanation for altruism towards non-kin proposes that it evolved as a reliable signal of individual quality to others, including potential mates. It is thus possible to see altruistic traits as ‘handicaps’ that act as indicators of the phenotypic and genetic quality under sexual selection. Here, I also suggest that sexual selection mechanisms other than the ‘handicap principle’ might have favoured the evolution of altruism towards non-kin.

I focus on human altruistic traits and speculate that the expansion of the brain in human evolution would have made increasing levels of parental investment essential. If displays of altruism towards non-kin had correlated with sustained parental investment then conditions particularly favourable to the evolution of altruistic traits could have existed. I make three predictions based on this scenario, each of which requires measurement of mate preference towards altruistic traits. I therefore develop and test a psychometric scale to measure this mate preference. Firstly, I predict that mate choice on the basis of altruistic traits will be found, a prediction supported in one sub-sample. Secondly, I predict significantly stronger female mate preference towards altruistic traits, a prediction that is also supported. Finally, I predict that, in line with sexual selection theory, variation in mate preference and preferred trait will be subject to genetic influence. This prediction is supported in a twin study of responses to the scales employed.

I also examine one form of altruistic behaviour – voluntary activity on behalf of others – and measure six possible motivations to perform this behaviour. I conclude that one motivation alone, altruistic motivation, accounts for volunteer commitment.

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CHAPTER 1: THE PROBLEM OF ALTRUISM

1.1 Introduction

1.1.1 The Concept of Altruism

The term altruism was invented by the French sociologist, Auguste Compte (1798-1857), who used the word to denote the benevolent as opposed to the egoistic or selfish tendencies in humans. Since that time altruism had been used by biologists in a rather different sense to describe behaviour in any species that is to the disadvantage of the altruist but to the benefit of other organisms. For some, why and how altruistic behaviour occurs in humans goes to the very heart of what it is that makes humans 'good' or 'bad'. For others, particularly evolutionary biologists, altruism is a puzzle that lies at the very centre of our understanding of how evolution works. Altruism is thus a topic that ranges across academic boundaries, having relevance to biology, moral philosophy, the social sciences and evolutionary psychology. While this thesis will focus purely on the biological causes of human altruism it nevertheless has wider implications for how humans see themselves and nature in general.

1.1.2 Darwin's View of Altruism

Altruism or selfless behaviour has been defined as any act that has the effect of increasing the chances of survival or reproductive success of another organism at the expense of that of the altruist (Ridley & Dawkins 1981). Yet Darwin's (1859) theory of evolution predicts vigorous competition between individual organisms on the basis that:

> ‘as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life’ (Darwin 1859, p.117).

As competition appears to be an inevitable condition of nature, evidence of altruistic behaviour seems, at first sight, to contradict evolutionary theory – and, therefore, all of modern biology. Darwin was aware of the problem of altruism at the very heart of his theory, describing it as ‘a special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory’ (Darwin 1859). He discussed possible solutions to it often using examples from human evolution and in ways that parallel the debates of modern times. He suggested that:

> ‘When two tribes of primeval man…. came into competition, if (other circumstances being equal) the one tribe included a great number of courageous, sympathetic and faithful members, who were always ready to warn each other of danger, to aid and defend each other, this tribe would succeed better and conquer the other.’ (Darwin 1871, p.155)

thereby speculating along the lines of group selection (Wynne-Edwards 1962). But in the very next paragraph Darwin recognised the weakness of such an approach:

‘It is extremely doubtful whether the offspring of the more sympathetic and benevolent parents, or of those who were the most faithful to their comrades, would be reared in greater numbers than the children of selfish and treacherous parents’ (Darwin 1871, p.155).

He then went on to suggest what we recognise today as reciprocity theory:

‘each man would soon learn that if he aided his fellow–men, he would commonly receive aid in return. From this low motive he might acquire the habit of aiding his fellows; and the habit of performing benevolent actions certainly strengthens the feeling of sympathy which gives the first impulse to benevolent actions. Habits, moreover, followed during many generations probably tend to be inherited.’ (Darwin 1871, p.156).

As Cronin (1991, p.328) comments, we must conclude:

‘that when Darwin dealt with human altruism, he saw the problem, he discussed it, but he nevertheless left it unsolved’.

1.1.3 Modern View of the Problem of Altruism

For a long period after Darwin’s death the acuteness of the problem posed by altruism received little attention because of the prevailing view in biology that individuals act for ‘the good of the species’ (Wynne Edwards 1962). By such logic examples of altruistic behaviour could thus be easily explained. The notion that selection took place at the level of the group was finally challenged in the 1960s and 1970s by Maynard Smith (1964), Williams (1966), Dawkins (1976) and others. Their grounds were simple and compelling. Altruistic groups may survive better than groups made up of selfish individuals but within such groups selfish organisms would tend to leave more offspring as a result of selfish behaviour favouring their fitness. As Maynard Smith put it:

> ‘‘anti-social’ mutations will occur, and any plausible model of group selection must explain why they do not spread’ (Maynard Smith 1964).

Mathematical models have demonstrated that selection at the group level is almost always slower than that at the individual level – so genes coding for selfish behaviour will be favoured by natural selection on this basis (Maynard Smith 1964, Dawkins 1976, Wade 1977, Ridley & Dawkins 1981). Williams (1966) and Dawkins (1976) have suggested that the gene, and not the individual, is the final unit of selection as it is genes that are transmitted across generations. On this basis, individuals can only be seen as temporary ‘vehicles’ (Dawkins 1976) for the transmission of genes, which are what are replicated and whose frequency may increase or decline over evolutionary time. The uncomfortable problem of altruism was thus brought back into clear focus – how could genes coding for altruistic behaviour possibly survive in a world where Darwinian logic dictated that only ‘the selfish gene’ would triumph? As Dawkins puts it:

‘at the gene level, altruism must be bad and selfishness good…Genes are competing directly with their alleles for survival since their alleles in the gene pool are rivals for their slot on the chromosomes of future generations .’ (Dawkins 1976, p. 38)

1.2 Inclusive Fitness

An important answer to this question was provided by Hamilton (1963, 1964) who demonstrated that genes can be favoured by natural selection not only if they cause their bearers to leave more offspring but also if they cause their bearers to increase the survival chances of their genetic relatives. Using simple genetics, Hamilton calculated the probability that an organism will share a gene with a relative (e.g. 0.5 with a parent or full sibling, 0.25 with a grandparent or grandchild) - a probability he termed the coefficient of relatedness (r). Whether a gene spreads in a population is not due to a certain behaviour being to the benefit of the individual but because it is for the benefit of the gene coding for it. Thus where a relative performs an altruistic act that helps another relative, and they share a gene coding for altruism towards relatives, the act can be explained in terms of promoting the fitness of that gene.

To this logic Hamilton added the requirement that the cost to the altruist (c) must be less than the benefit to the recipient (b) and then proposed that altruistic acts would occur where $rb > c$ or $K > 1/c$, where K is the benefit to cost ratio. This has become known as Hamilton’s rule and the concept on which it is based - referred to as kin selection or inclusive fitness - has become widely accepted in biology and supported by empirical evidence (Madsen et al 2007). While this consensus may still be open to criticism (Zahavi & Zahavi 1997, p. 164) I shall not consider it further in this thesis.

1.3 Reciprocal Altruism

1.3.1 Reciprocal Altruism

The problem of accounting for altruistic behaviour towards non-relatives, however, remains. Examples of such behaviour include mutual grooming among unrelated primates (Boyd & Silk 1997), giving warning calls of nearby predators to unrelated individuals (thus putting the caller at greater risk) (Boyd & Silk 1997) and numerous cases of human altruism towards non-kin (e.g. Millot 1971; Alexander 1979; Goldberg 1995; Becker & Eagly 2004). The first major attempt to answer this problem was the theory of reciprocal altruism proposed by Trivers (1971). He envisaged that, in conditions where the same individuals interact repeatedly over time, an altruistic act by one individual might be reciprocated at a later stage by the other, thus promoting the fitness of any gene linked to this process. The benefit of the altruistic act to the recipient must be greater than the cost to the altruist with the result that an ongoing exchange of altruistic acts with the correct cost/benefit ratio would favour genes coding for altruistic behaviour towards non-kin.

Trivers (1971), however, identified a difficulty with reciprocal altruism – that certain individuals might 'cheat' by failing to reciprocate or by reciprocating in ways that limited their cost to fitness and the benefit to the other altruist. Genes linked to this form of cheating would be liable to undermine the selective process as surely as selfish genes would undermine group selection. Trivers (1971) suggested that selection could discriminate against such cheating if those individuals suffered later adverse effects that outweighed the benefit of not reciprocating. This could occur if the altruist curtailed all future altruistic acts towards the cheating individual and thus the cheater would be selected against as a result of this ‘punishment’.

1.3.2 The Prisoner’s Dilemma (IPD) Model

Acceptance of the theory of reciprocal altruism was greatly helped by associated work based on the Iterated Prisoner’s Dilemma (IPD) model which is intended to be a simplified formulation of how mutual co-operation could evolve in a world of selfish individuals (Axelrod & Hamilton 1981, Axelrod 1984, Axelrod & Dion 1988). It is based on the conflict of interests between two hypothetical prisoners being interrogated by the police in separate rooms. If both refuse to blame the other for the crime each receives only a modest sentence, as the police evidence against them is not compelling in this imaginary situation. But if one blames the other prisoner and that prisoner continues to keep quiet the confessing prisoner is let off scot-free and the prisoner who remains silent receives a maximum sentence.

Thus the two prisoners (or players) have a choice as to whether to cooperate (by helping each other through their silence) or not to cooperate (in the terms of the model, to ‘defect’ for selfish reasons by giving the police their evidence). The requirements of the model are such that the payoffs represent the respective rewards for cooperation or defection. These are arranged so that $T > R > P > S$ where T is ‘temptation’ to defect where the other player chooses cooperation, R is the ‘reward’ for mutual cooperation, P is ‘punishment’ where both players defect and S is the 'sucker's payoff' where the player cooperates while the other defects. The payoffs are also arranged so that:

$$R > \frac{T + S}{2}$$

where the reward for cooperation is greater than half the sum of Temptation and Sucker's Payoff. The respective payoffs accruing to the players under the IPD are illustrated in Figure 1.1 (Axelrod 1984).

Figure 1.1. Payoffs resulting from the Iterated Prisoner's Dilemma (IPD) model

		Column Player	
		Cooperate	Defect
Row Player	Cooperate	$R = 3, R = 3$ Rewards for mutual cooperation	$S = 0, T = 5$ Sucker's payoff and temptation to defect
	Defect	$T = 5$, S = 0 Temptation to defect and sucker's payoff	$P = 1, P = 1$ Punishment for mutual defection

In any single interaction it will always pay both players to defect but where they interact over an indefinite number of times, and the players cannot be sure when the last interaction will occur, the potential for cooperation can emerge (Axelrod 1984, p. 10-11). This means that a choice made in the present not only determines the outcome of this move but can also influence the later choices of players. The importance or weight (w) of the next move relative to the current move represents the degree to which the payoff of each move is discounted relative to the previous move.

These interactions between two players are repeated for an indefinite period of time during which each player accumulates a score on this basis.

Computer simulation was then employed to determine the optimal strategy under the conditions of the IPD model. A ‘computer tournament’ in which numerous strategies were put in competition with each other (Axelrod 1984) confirmed that a strategy called ‘tit for tat’ (TFT) (Axelrod & Hamilton 1981) was most successful over the long term. The TFT strategy required a player to cooperate on the first move and then copy whatever the other player did in response from that point onwards. It can be seen that the successful TFT strategy broadly mimicked the principle of what Trivers (1971) had proposed earlier under reciprocal altruism. The coincidence of these two independently arrived at pieces of theory, combined with the optimistic message that ‘nice’, ‘forgiving’ organisms succeed in nature, gave reciprocity theory an alluring persuasiveness. The IPD model soon became the ‘orthodox paradigm’ to account for the evolution of cooperation among non-relatives (Dugatkin et al 1992) and reciprocity theory achieved a consensus among most workers in the field as the means by which altruism towards non-kin could be explained by Darwinian theory.

1.3.3 Problems with Reciprocal Altruism Theory and the IPD Model

Subsequent work, however, began to cast doubt on how relevant reciprocal altruism and the IPD model was to much of what occurs in nature:

- *Reciprocal altruism is less likely where more than two-person interactions take place.* Mathematical modelling found that reciprocal altruism became increasingly unlikely as group size increased (Axelrod & Dion 1988; Boyd & Richerson 1988, 1992).

- *Timeframe for decision-making in nature.* The model requires more or less simultaneous decisions by players while in nature such decisions are rare with individuals usually assessing potential partners over time before any cooperation begins and using communication in the process (Noe 1990; Dugatkin et al 1992; Zahavi 1995; Noe 2006).
- *There is difficulty in measuring the costs and benefits in any reciprocal interaction.* A serious problem in modelling the development of reciprocity lay in demonstrating the costs and benefits involved (Noe 1990; Roberts 1998). For example, there may be variation in the currencies of reciprocation (providing food now may be paid back later by access to mates) and in the time taken to reciprocate ('later' may range from several minutes to several months) (Barnard 2004, p.627-628).
- *The issue of 'cheating' remains difficult to resolve in the case of 'second order cheating'.* Sigmund (1993) drew attention to the problem of individuals who reciprocate with altruists with whom they have interacted but do not then punish those who have cheated others (i.e. 'second order cheating'), thus undermining the process. It has been suggested (Zahavi & Zahavi 1997, p.132) that those who punish 'second order cheating' are, in effect, altruists acting on behalf of the group. Thus the enforcement mechanism that 'explains' altruism itself presupposes the existence of altruism, thereby exposing a fallacy at the centre of the reasoning. Possible solutions to this problem include 'meta-punishment' (Boyd & Richerson 1992), group selection (Wilson & Sober 1994; Boyd et al 2003) 'image

scoring' or reputation (Nowak & Sigmund 1998; Leimar & Hamerstein 2001) and 'costly signalling' (Gintis et al 2001), some of which are discussed further below.

- *How could reciprocity get started in a world of selfish individuals?* While the maintenance of reciprocal altruism may be explicable, it is difficult to envisage how genes coding for such behaviour could have evolved in an existing population of selfish individuals, given that at least two unrelated altruists would be needed to start the process – an apparently unlikely event. Various explanations have been put forward. It could have emerged as part of kin selection, which might then have been generalised to non-relatives (Krebs & Davies 1993, p. 260-261) or by local clusters of individuals with genes coding for reciprocity (Boorman & Levitt 1980). Game theory has been used to demonstrate that an invasion barrier can be overcome by a mass of TFT players (Nowak & Sigmund 1992) and that, with an intermediate population size, TFT can invade and replace a population of defectors (Nowak et al 2004).

1.4 Further Developments of Reciprocity Theory

1.4.1 Indirect Reciprocity

The notion of 'indirect reciprocity' was an attempt to solve the problem of 'second order cheating' and has been developed by Nowak and Sigmund (1998) and Leimar and Hammerstein (2001), among others, based on an idea first put forward by Alexander (1979). It relies on the 'image' or reputation of an altruist conferring a selective advantage on that individual in terms of the behaviour of other members of that population towards that individual. It depends crucially on ‘image score’ or the reputation of an individual as an altruist or non-altruist being accurately known by every other member of a group – even if a particular altruistic act is not reciprocated. In contrast to reciprocal altruism, the ‘indirect reciprocity’ model avoids the need for the same two individuals to meet again with selection favouring cooperative strategies that reward those who have helped others in the past. Thus the likely future behaviour of others towards potentially selfish individuals is seen as deterring selfish behaviour, including ‘second order cheating’. Nowak and Sigmund’s (1998) model provides an answer to some of the weaknesses in reciprocal altruism theory discussed above - although it has been criticised by others who question its evolutionary stability (Leimar & Hammerstein 2001). Furthermore, game theory modelling has been unable to account for how an indirect reciprocity strategy can invade a population in which it has not already been established (Panchanathan & Boyd 2004).

1.4.2 ‘Costly Signalling’

Current thinking and game theory modelling is nevertheless usually based on some version of indirect reciprocity rather than the early version of reciprocal altruism suggested by Trivers (1971). One advance in indirect reciprocity theory is the ‘costly signalling’ model put forward by Gintis et al (2001). This model is influenced by Zahavi’s ‘handicap principle’ (Zahavi 1975; Zahavi & Zahavi1997) where the underlying genetic and phenotypic quality of an individual is seen as most accurately assessed by the ‘honesty’ or reliability of the ‘signal’ sent to others. Using a multiplayer game theory model, Gintis et al (2001) tested the notion that cooperation evolved as an ‘honest’ signal of individual’s quality as a potential ally, competitor or mate within a group. Through the ‘honesty’ of the signal of cooperative behaviour Gintis et al (2001) were able to show that such a process could deal successfully with cheating, including particularly ‘second order cheating’, and, furthermore, could proliferate when rare.

1.4.3 The ‘Raise the Stakes’ Strategy

Roberts and Sherratt’s (1998) notion of a ‘raise the stakes’ strategy is based on the plausible assumption that altruistic co-operation is rarely an ‘all or nothing’ behaviour but one characterised by a relationship of matching altruistic investment by the individuals involved. Roberts and Sherratt (1998) found that a model where altruistic investment increases correspondingly with a partner who matches or betters the last move (or investment) was successful one. The key claims here are that the ‘raise the stakes’ strategy is both resistant to cheating and capable of invading a population of non-altruists, thus providing another answer to the weaknesses seen in reciprocal altruism theory.

1.4.4 ‘ Competitive Altruism’

Roberts (1998) has also used Zahavi’s handicap principle (Zahavi 1975; Zahavi & Zahavi 1997) in the context of altruism being seen as an ‘honest’ signal of underlying quality. He has suggested that individual differences in generosity are associated with competition for partners and alliances and thereby to an escalation in generosity (Roberts 1998). Evidence consistent with the predictions of the competitive altruism model has been found (Hardy & Van Vugt 2006).

1.4.5 'Strong Reciprocity'

These indirect reciprocity models have, however, encountered one difficulty. A human cooperation conducted by Fehr & Gachter (2002) has demonstrated that altruistic behaviour can persist in a context where reciprocation or reputation formation are not possible – that is, in one-off, anonymous encounters with others. Under these experimental conditions reciprocation, reputation formation, 'costly signalling', matching reciprocation or 'competitive altruism' are not strictly possible (see Section 1.6.2 for detailed discussion of the experiment). Such behaviour has been termed 'strong reciprocity' and can be defined as a willingness to sacrifice resources in rewarding fair behaviour and punishing unfair behaviour even if this is costly and provides no present or future rewards (Fehr & Henrich 2003).

One explanation for 'strong reciprocity' is that it arose as a result of group selection. Envisaging that groups would have periodically faced extinction-threatening events in evolution, Gintis (2000) developed a model that compared the performance of groups in these situations. He found that groups containing a sufficiently high proportion of strong reciprocators were able to induce even self-interested individuals to cooperate. Gintis (2000) concluded that 'strong reciprocation' could have been favoured by group selection through groups containing a sufficiently high proportion of them avoiding extinction (Gintis et al 2007).

Others (Johnson et al 2003) have argued that examples of ‘strong reciprocity’ revealed in Fehr & Gachter’s (2002) experiment can be explained by the rareness with which such situations would have occurred in the evolutionary past and the consequent likelihood that reciprocal behaviour is ‘misfiring’ in these experimental situations. Such an interpretation has been challenged by those (Fehr & Gachter 2003; Fehr & Henrich (2003) who deny that the frequency of one-off encounters between non-relatives in the evolutionary past would have been very different to the present day.

1.5 Empirical Evidence for Reciprocity and Indirect Reciprocity in Non-Humans

1.5.1 Blood Sharing in Vampire Bats (Desmodus rotundus)

Firstly, I consider some of the key evidence cited in favour of reciprocity and indirect reciprocity in non-human species. Evidence for such theory in humans will be discussed later. A study of food sharing among vampire bats is an often-cited example of reciprocity (Wilkinson 1984). These creatures live in all-female groups mostly containing close relatives but also some unrelated females who are recruited, on average, once every two years. They feed at night by gorging on blood but sometimes they fail to do so – an outcome that can be fatal. Wilkinson (1984) found that hungry vampire bats returning to their roost were often fed by other bats who regurgitated blood to save the hungry individual. Of 110 cases of regurgitation observed, 77 were between mother and nursing offspring. In 21 other cases, where degree of relatedness was unknown, an index of opportunity for reciprocity between the recipient and every other bat was used (Wilkinson 1984). From this evidence Wilkinson inferred that reciprocation between non-kin was occurring. In a separate piece of research, captive vampire bats, who were known to be unrelated, were found to regurgitate blood significantly more often to those who had donated blood previously. Nevertheless some have criticised the study on the grounds that kin selection cannot be ruled out as the sole cause of blood regurgitation in the wild (Noe 1990, Shettleworth 1998).

1.5.2 Coalition Formation in Male Olive Baboons (Papio anubis)

The difficulty of separating the effects of kin selection from reciprocal altruism was largely overcome in a study of male olive baboons (Packer 1977) for in this species males breed in troops of individuals who have transferred from elsewhere. Packer observed coalitions in which an ‘enlisting’ male ‘solicited’ help from another male against an opponent in order to gain reproductive access to a female who was consorting with the opponent. Once the coalition was formed the ‘solicited’ male generally continued to fight the opponent - at some risk of injury to himself – while the ‘enlisting’ male impregnated the female. The study found that previous partners were ‘solicited’ significantly more often than average, suggesting a process that may be at least partly based on reciprocation. However, this study has been criticised on grounds of the paucity of the evidence and the absence of clear-cut evidence for retaliation against cheating (Noe 1990).

1.5.3 ‘Egg Trading’ in Black Hamlet Fish (Hypoplectrus nigricans)

Another case claimed to be an example of reciprocity is spawning behaviour among black hamlet fish (Krebs & Davies 1993, p. 280) based on an original study by Fischer (1980). All individuals of this species have both male and female gonads and thus each individual is able to provide both eggs and sperm. However, eggs are more costly to produce than sperm and so it is in the selfish interests of each individual to provide sperm when two partners interact in spawning behaviour. However, Fischer (1980) found that after an individual had found a partner each released only a portion of eggs at any one time in an alternating process of eggs and sperm production. Where a partner failed to reciprocate by providing eggs after providing only sperm the other individual refused to give up any more eggs and left.

1.5.4 Predator Inspection in Sticklebacks (Gasterosteus aculeatus)

Another context in which 'tit for tat' reciprocity has been seen as present involves predator inspection by three-spined sticklebacks (Milinski 1987). In the wild, tentative inspection of predators is typical among this species, followed by a rush back to the shoal when the predator moves towards the inspector. In an experiment, a system of mirrors in a tank simulated a cooperating or defecting companion who accompanied a stickleback as it approached a live predator located in another partition of the tank. Milinski was able to demonstrate that where the mirror simulated a cooperating companion the stickleback moved to the front half of the tank twice as often as with a defecting companion, thus apparently providing evidence for a 'tit for tat' strategy.

Milinski's interpretation has been challenged by Lazarus and Metcalfe (1990), who pointed out that more parsimonious explanations could account for the evidence. They suggested that having a companion would reduce the risk of capture by a predator, a point borne out by Milinski's own evidence that, in the wild, inspectors in groups of two got closer to the predator than when alone (Milinski 1990). Lazarus and Metcalfe also saw that the greater boldness when in the presence of a 'reciprocating' companion might simply be a reflection of the stickleback's tendency to shoal. This point has been supported by Masters and Waite (1990) who found the same behaviour pattern persisted when no predator was present in the other tank. Godin and Davies (1995) have also argued against Milinski's inference of reciprocal altruism in predator inspection, pointing out that several studies have shown that predator inspections in fish are either equally or more frequently made by solitary individuals. It has also been argued that predator inspection does not resemble the IPD model upon which the experiment was based (Noe 2006). Milinski (1990) has contested these arguments and Dugatkin (1997, p. 67-70) has carried out a number of experiments in response to these criticisms where he concluded that predator inspectors were using something akin to 'Tit for Tat'.

1.5.5 Grooming and Aid in Vervet Monkeys (Cercopithecus aethiops)

Seyforth and Cheney's (1984) study of grooming behaviour in vervet monkeys involved playbacks of calls soliciting support when threatened by other individuals. Grooming is the most common form of affinitive behaviour in primates and usually occurs between close relatives. However, they found that where grooming had recently taken place between non-kin it increased the probability that the individuals concerned would attend to each other’s solicitations for aid. This was seen as an example of reciprocity among non-kin, although still dependent on the relative dominance rank of the potential opponent.

1.5.6 ‘Lead’ and ‘Lagging’ Behaviour in Lions (Panthera leo)

In two studies, male (Grinnel et al 1995) and female (Heinsohn & Packer 1995) lion prides were observed responding to the simulated playing back of the recorded roars of other prides intruding into their territory. Challenging this intrusion resembled an IPD in that those at the front of the group (i.e. those who ‘led’), were more likely to be killed or injured in such territorial disputes (Heinsohn & Packer 1995), and could be seen as co-operators while those ‘lagging’ behind could be seen as defecting. But in repeated playbacks both studies found that the same individuals consistently either ‘led’ or ‘lagged’ in the playback responses. Thus these experiments demonstrated an absence of reciprocity (Legge 1996) even where, in the case of female lions, the individuals were closely related.

1.5.7 Empirical Evidence: Conclusion

Clearcut empirical evidence in favour of reciprocity or indirect reciprocity among non-human species therefore appears sparse or equivocal (Degler 1991; Brembs 1996; Boyd & Silk 1997). Where studies have suggested it is present (e.g. Milinski 1987; Packer 1977; Wilkinson 1984) some of these claims have been questioned (Lazarus & Metcalfe 1990; Masters & Waite 1990; Noe 1990; Godin & Davis 1995; Hammerstein 2002) with some of the evidence possibly explainable by the influence of kin selection (Noe 1990; Shettleworth 1998). A number of workers have gone on to point to the marked contrast between the large volume of game theory modelling carried out over the last thirty or more years and the relative lack of empirical evidence found to support that theory (Hammerstein 2002; Stephens et al 2002; Fehr & Fischbacher 2003). As Stephens et al (2002) have put it:

‘More than 20 years after Axelrod declared IPD to be ‘ the *E. coli* of social psychology’ there is still no single unambiguous case of stable nonhuman cooperation in a verifiable Prisoner’s Dilemma’.

In discussing whether reciprocity represents what happens in nature, Dugatkin (1997), felt able to conclude:

‘My guess is that, in the long run, the answer will probably be a resounding ‘No’.’

Nevertheless the consensus remains that altruism towards non-kin is a problem that needs to be solved in non-human species and that reciprocity or indirect theory offers the best current solution to it. I conclude that we are still a long way off from establishing a sound basis of empirical evidence in favour of such theory.

1.6 Reciprocity Theory and Human Behaviour

1.6.1 The Apparent Commonness of Reciprocity among Humans

Despite the arguments above, evidence for reciprocity and indirect reciprocity among humans is generally considered to be extensive and well founded (Wilson 1975; Broude 1999; Krebs 2000; Milinski et al 2001; Milinski et al 2002), with reciprocity and cooperation seen as fundamental to all human societies (Axelrod 1984; Laland & Brown 2002; Fehr 2004). One example, often cited, of the survival of cooperation in unlikely circumstances is the 'live and let live ' system that developed between soldiers of opposing side in the trench warfare of the First World War (Axelrod 1984), until finally suppressed by the high command. This has been interpreted as an important example of an IPD model working in practice (Axelrod 1984), although I would argue that it is better seen as an example of mutualism (see Section 1.8.4).

Nevertheless examples of selfishness in human affairs abound, leading to poor outcomes for all concerned. Examples include the so-called 'tragedy of the commons' (Hardin 1968) and states erecting trade barriers in adverse economic times that, in the long term, reduce their common prosperity still further (Axelrod 1984, p. 7).

1.6.2 Evidence at Odds with Reciprocation as the Basis for Human Altruism towards Non-Kin

Examples can be found in modern industrialised societies of where altruistic behaviour towards non-kin is present but reciprocation by the recipients is neither possible nor expected. Alexander (1979) has pointed to the example of blood donation as altruism without reciprocity. Donation to beggars or panhandlers is unlikely to result in reciprocation by those receiving the gift (Goldberg 1995).

Extreme examples of human altruism, such as suicide by Japanese kamikaze pilots during the Second World War, also did not appear to involve an expectation of reciprocation by the altruists (Millot 1971). The suicidal behaviour appears to have been provoked by the frustration of pilots at not being able to sink allied ships and was not instigated by higher-ranking commanders (Millot 1971). People come to each other's rescue in crises and disasters where reciprocation appears unlikely (Becker & Eagly 2004). In all of these examples, however, reputation or other aspects of indirect reciprocity (e.g. 'costly signalling' or 'competitive altruism') may still have influenced altruistic behaviour. Donation to public collections for charity is another example of where reciprocation is neither possible nor expected and yet indirect reciprocity may well be involved in the altruistic behaviour.

As discussed above, a study by Fehr and Gacher (2002) has provided evidence of the human capacity to behave altruistically under the conditions that appear to be at odds with both reciprocity and indirect reciprocity theory. This human cooperation experiment involved subjects being asked to 'invest' real money into a project in groups where all gained a reward for that investment regardless of whether or not they contributed to the investment. Thus it was always in the material self-interest of subjects not to 'invest' (i.e. defect or act selfishly), although, if all acted for the good of the group, they would gain a greater benefit in total. Decisions were anonymous and simultaneous. However, in one condition, subjects were told of the decisions of other fellow group members and given the opportunity to 'punish' a group member at a financial cost to themselves. Most acts of 'punishment' were imposed on below average contributors to the group by above average contributors and occurred where no subject ever met another subject more than once. In fact, 'punishment' of non-co-operators substantially increased the amounts subsequently invested. Thus the only subjects to benefit were future members of a ‘punished’ subject’s group who might, as a result, enjoy increased investments by the punished non-co-operators in future stages of the experiment.

The key point from Fehr and Gachter’s study (2002) is that altruistic ‘punishment’ was found to occur in anonymous, non-repeated interactions where gains from reputation were small or absent – that is, where conditions required by indirect reciprocity theory for altruistic behaviour to occur were not present (although see Johnson et al 2003). A re-interpretation of Fehr and Gachter’s data which suggested that subjects were punishing high earners rather than non-compliance (Fowler et al 2005) does not deal with the central question of why they behaved altruistically in punishing high earners.

1.6.3 Meat Acquisition in Modern Hunter/Gatherer Societies

It is not just in modern industrial societies, however, where evidence is available of human altruistic behaviour that is at odds with reciprocity as the basis for human altruism towards non-kin. Studies of modern hunter-gatherer societies are important in that they may reflect an environment similar to that in which humans evolved, although one still needs to be cautious in applying present-day findings to past periods (Landers 1994). Within these societies the acquisition and sharing of food should provide a key example of human reciprocity. However, both Kaplan & Hill (1985) and Hawkes (1991) found no evidence for reciprocity in meat acquisition in modern hunter-gatherer societies, although both pointed to evidence that certain other social benefits might accrue to the successful hunter (Kaplan & Hill 1985; Hawkes 1993). It has also been suggested that evidence over a longer timescale may reveal that reciprocation in kind is taking place (Hill & Kaplan 1993 though see Hawkes 1993).

1.6.4 Conclusion on Reciprocity in Human Behaviour

The assumption that reciprocity and indirect reciprocity are basic conditions of human behaviour is thus called into question by these examples. I therefore conclude that we are entitled to explore alternative theory to test whether it might better account for these instances of human altruistic behaviour.

1.7 Why Reciprocity may be Rare in Nature

1.7.1 Trivers' Six Parameters

In his original formulation of reciprocal altruism Trivers (1971) specified six parameters that he saw as affecting whether reciprocity would be favoured by selection:

1) length of lifetime (individuals of longer–lived species are seen as more likely to interact frequently and therefore reciprocate);
2) dispersal rate (low dispersal rate is seen as increasing the chance of repeated interactions between individuals and thus reciprocation);

3) mutual dependence (high inter-dependence is seen as promoting interactions and reciprocation);
4) parental care (reciprocity also seen as possible between close kin);
5) dominance hierarchies (seen as reducing the opportunity for reciprocal interactions);
6) aid in combat (coalitions between individuals seen as reducing asymmetry in power and status and thus promoting reciprocity).

In many species these parameters may well combine to create conditions that are not favourable to the evolution of reciprocal altruism. One condition particularly likely to restrict its evolution is that specified under parameter 5, where Trivers comments:

> ‘Strong dominance hierarchies reduce the extent to which altruistic situations occur in which the less dominant individual is capable of performing a benefit for the more dominant which the more dominant individual could not simply take at will.’ (Trivers 1971)

Trivers argued that while linear dominance hierarchies are typical of some species they are less evident in others. He contrasted meat sharing in baboons (*Papio cynocepahalus*), where the meat is simply seized by the dominant male, with chimpanzees (*Pan troglodytes*) who are seen as a ‘less dominance-oriented’ species in this respect. He cited the ‘begging gestures’ by more dominant chimpanzees towards less dominant individuals who have acquired portions of the hunted meat (though see Nishida & Hiraiwa-Hasegawa 1986). Trivers then went on to suggest that early hominids would have been likely to have experienced a similar dominance system to that of modern chimpanzees and so would have evolved in an environment where dominance hierarchies would have been less developed.

1.7.2 The Widespread Nature of Asymmetry in Power and Status

Asymmetry or inequality in power and status among individuals has been observed in a wide range of species at all taxonomic levels (West-Eberhard 1975; Dunbar 1988) and takes many forms (Wilson 1980, p. 137-140, Boyd & Silk 1997, p. 212 – 241) with asymmetry in power and status between group-living individuals seen by some as typical in nature (Gould & Gould 1989, p.141). On the other hand, there are many primate species where dominance hierarchies are unclear, ambiguous or apparently non-existent (Walters & Seyforth 1986).

In terms of the examples chosen by Trivers, it would be difficult to characterise chimpanzees as a species where there is symmetry or equality in power and status between individuals, as hierarchies, albeit of a loose and informal kind, have been observed in this species (Goodall 1986). Modern hunter-gatherer societies have often been seen as egalitarian with no differentiation in social status or occupation (Boehm 1999). Yet recent research has indicated that differences in status are present, based on variation in hunting success, and that these are correlated with variation in reproductive success (Smith 2004) and better offspring survival (Kaplan & Hill 1985; Hill & Hurtado 1996). If these studies provide an accurate insight into the conditions under which humans evolved then it is by no means certain that relative symmetry in power and status would have been typical of hominid societies during human evolution, as Trivers suggested.

Trivers also proposed (condition 6 above) that coalitions between less dominant individuals in aggressive encounters can lead to relatively symmetrical power relations, citing the examples of alliances observed within certain primate species (e.g. baboons and vervet monkeys). However, the question arises as to whether individuals within the coalition revert to asymmetry in power and status once the immediate goal of the coalition has been achieved (e.g. a takeover of a group). There is evidence that a single alpha male takes over within coalitions (Boehm 1999, p. 25), a conclusion borne out, for example, among baboons where strong coalition members gain most of the benefits (Noe 1990). On the other hand, there is an example of coalitions among subordinate paper wasps (*Polistes fuscatus*) successfully challenging the dominant queen when she eats too many of their eggs (Reeve & Nonacs 1992). The degree to which coalitions can promote symmetrical power relationships between coalition members is thus open to question.

1.7.3 Asymmetry in Power and Status and the IPD Model

Asymmetry in power and status may present a particular problem for the IPD model upon which so much theoretical modelling has been based. In its original formulation, both prisoners (or players) are in a position of identical power in relation to each other and the police. Each has the power to apply just one sanction to the other (i.e. defect by blaming the other). If one attempts to reflect any asymmetry in power and status in the relationship between the two players then the arithmetical balance upon which the IPD model is based may be affected as follows:

- the payoff to the more powerful player for cooperation is likely to be reduced in so far as that player can gain whatever reward is desired without the need for cooperation;
- the option to the less powerful player of punishing the more powerful player becomes restricted should that player not reciprocate in due course.

A situation where one player has more power and status than the other is likely to entail a very different range of payoffs (i.e. 'Temptation' T would be greater for the more powerful player while 'Punishment' P would be reduced for the less powerful player). Modelling of such asymmetry is needed to fully understand its likely consequences. This might raise the question of whether a 'tit for tat' strategy remains optimal under conditions where the assumption of symmetry in power and status is relaxed.

1.7.4 Indirect Reciprocity Theory and Asymmetry in Power and Status

Indirect reciprocity theory (Alexander 1979; Nowak & Sigmund 1998; Gintis et al 2001; Leimar & Hammerstein 2001) relies on the reputation or 'image score' of an individual to promote altruistic behaviour towards other group members. Yet where asymmetry in power and status exists this also raises a question about how successfully such models might work. Less dominant individuals may not be in a position to reduce the survival and reproductive success of a more dominant individual who has acquired a poor reputation or 'image score'. In relation to the 'costly signalling' model (Gintis et al 2001) any selective advantage through favourable treatment by mates, same sex partners or competitors in response to altruistic behaviour on behalf of the group is likely to be outweighed by the selfish behaviour of more dominant group members. The possibility of dominant or aggressive behaviour towards other group members evolving under this model instead of altruism – a possibility discussed by Gintis et al (2001) – might well be an outcome in this context linked to inequality in power and status. By the same token, the assumption of a matching investment by two players under the 'raise the stakes' strategy (Roberts & Sherratt 1998) could be violated if there was a markedly asymmetric power relationship between them.

1.7.5 Conclusion on Why Asymmetry in Power and Status May Affect Opportunities for Reciprocity to Develop

It is surprising that the literature on altruism has not given more recognition to the issues raised by asymmetry in power and status - and the other parameters proposed by Trivers – in restricting scope for the evolution of reciprocity. Maynard Smith (1982), in specifying the requirements for co-operation to evolve by means of a 'tit for tat' strategy, confirmed that each individual must be able to retaliate against defection by the other – an option likely to be restricted in these cases. Axelrod (1984, p.149-154) discussed dominance hierarchies in relation to the IPD model in terms of a situation where there is a 'bully' who often defects but never tolerates a defection from the other player. However, he did not appear to recognise the difficulty this behaviour might represent for the IPD model. Noe (1990) recognised inequality in power and status between coalition members in his 'veto game' model, based on patterns of coalition formation among male baboons. In this model, a 'veto player' has leverage due to an ability to 'play off' potential partners against each other, rather than any power based on dominance, phenotypic condition or fighting ability.

To sum up, more attention needs to be given to how asymmetry in power and status impacts on direct and indirect reciprocity models. Cases where two individuals have apparent symmetry in power in a particular context (e.g. ‘egg trading’ among black hamlet fish (Fischer 1980) are of particular interest here. It may be that this factor will come to be seen as explaining the rarity of examples of reciprocity and indirect reciprocity found in nature.

1.8 Alternative Explanations for Altruism towards Non-Kin

1.8.1 ‘New’ Group Selection

Another approach to explaining the problem of altruism has involved a re-examination of the principle of group selection (Wilson 1975; Wade 1977; Wilson & Sober 1994; Sober & Wilson 1998). Wilson (1975) has proposed that ‘trait groups’ or sub-groups of a population can exert varying effects on the fitness of the individuals within them. As such, ‘trait groups’ can be seen as ‘vehicles of selection’ in the same way that individuals were regarded as ‘vehicles of selection’ by Williams (1966) and Dawkins (1976). This approach thus still holds firm to the notion that the gene remains the ultimate unit of selection but it has introduced genetic models that partition variance into within-group and between-group components (Dugatkin & Reeve 1994; Dugatkin 1997).

Wilson (1975) used the analogy of warning calls of a nearby predator - with the assumption being made that the caller thereby increases the risk to itself and so performs an altruistic act in warning non-kin in the ‘trait group’ of the danger. The analogy illustrates the varying effects on fitness present at different levels for, although this altruistic act diminishes the survival chances of the altruistic caller, it increases the survival chances of all those in the ‘trait group’ compared with members of a ‘trait group’ containing no altruists. Thus groups with a large proportion of altruists will out-perform groups with a lower proportion of altruists who would be more subject to predation. With Wilson’s (1975) model of group selection, individuals are able to disperse and reform in new ‘trait groups’ in each generation in contrast with the traditional formulation of group selection where less successful groups simply become extinct (Wynne Edwards 1962). In such a manner Wilson was able to demonstrate that genes associated with more altruistic behaviour can increase in frequency in a population as a whole through group selection.

‘New’ group selection was also explored by the theoretical modelling of Wade (1977) who took a broad view of its effects without specifically focusing on altruistic behaviour. Other theoretical models have emphasised the importance of small groups and low migration between those groups to maintain between-group variation on which the process depends – thereby promoting altruistic cooperation (Boyd & Richerson 1985). Group selection has also been used to account for the evolution of altruistic punishment under reciprocity theory (Boyd et al 2003) and strong reciprocators increasing in frequency in a population (Gintis 1990; Gintis et al 2007).

This approach has also thrown fresh light on empirical studies of altruistic behaviour. Predator inspection (see discussion above of Milinski's (1987) study of sticklebacks) could plausibly be seen as an outcome of between-group selection in favour of inspection outweighing individual selection against it (Dugatkin & Reeve 1994). By the same token, 'lead' and 'lagging' behaviour in lions (Grinnel et al 1995; Heinsohn & Packer 1995), discussed above, could also be seen in the same light. Here, 'lead' behaviour that incurs increased mortality (Heinsohn & Packer 1995) might also benefit the group in terms of the speed and assertiveness of response to an intruding group challenging for territory. Observed behaviour might be the result of a trade-off between individual selection against altruistic behaviour and between-group selection in favour of it.

'New' group selection must, however, be able to deal with the point that continues to be raised against it. It is not that such selection cannot work but that it is likely to be rare under natural conditions (Barnard 2004, p. 67). It requires low levels of gene flow between groups, low mutation rates within groups and little likelihood of selfish 'cheats' exploiting their position within such groups - a combination of conditions likely to be rare (Barnard 2004, p. 67).

1.8.2 Memes and Memetics

It was Dawkins (1976, p.192-201) who suggested the concept of a cultural replicator or unit of imitation that he termed a 'meme'. He then drew an analogy with genes in so far as memes can propagate themselves 'by leaping from brain to brain via a process which, in the broad sense, can be called imitation' (Dawkins 1976, p.192).

This notion has subsequently been developed into a new field – memetics – that has been seen as relevant to the development of altruistic behaviour. It has been suggested that altruistic people become popular and, as a result, memes associated with altruistic behaviour become copied and thus have spread widely (Blackmore 1999, p. 155).

The concept of memes has, however, been criticised on the grounds that it is insufficiently precise, which is also seen as why memetics has yet to generate a distinctive body of research (Aunger 2007). Until progress in these two respects is made it is difficult to envisage memetics providing an incisive insight into understanding altruistic behaviour.

1.8.3 Gene/Culture Co-Evolution

The relationship between genetic and cultural influences has also underpinned an approach by Lumsden and Wilson (1981). Using a mainly mathematical method to explore a proposed co-evolution between genetic and cultural factors, they have suggested that the genetic fitness of an organism is determined not only by its genotype but also by its cultural heritage. Lumsden and Wilson envisage genes and culture interacting in a positive feedback loop during human evolution and resulting in 'culturgens', which they see as an array of 'transmissible' behaviours (Lumsden & Wilson 1981, p.7). Altruistic traits can thus be seen as an example of a 'culturgen' produced by such a process. Lumsden and Wilson's approach is one of a number of models that have sought to draw an analogy between genetic and cultural selection for traits, including altruistic ones (Barnard 2004, p. 592-602). A possible link between early human inter-group competition and gene/culture co-evolution has also been modelled (Bowles 2006).

1.*8.4 Mutualism*

Under some relationships between non-kin observed in nature, there is a mutual gain to those involved that may appear reciprocal but, in practice, involve no temptation to defect since that would result in a reduction in fitness for the would-be ‘cheat’ (Barnard 2004, p. 466). Such relationships have been termed mutualism (West-Eberhard 1975), by-product mutualism (Brown 1983) and pseudo-reciprocity (Connor 1986). The notion of mutualistic interaction has been taken further with the idea of ‘biological markets’ (Noe & Hammerstein 1995) where ‘traders’ in the benefits that one organism can offer to another compete to obtain the highest return so as to optimise reproductive success.

Empirical support for mutualism has been claimed in a study of blue jays (Clements & Stephens 1995) and territorial disputes among fiddler crabs (Backwell & Jennions 2004). It has been suggested that much apparently altruistic behaviour in the form of helping non-related offspring (such as ‘helping at the nest’) may carry with it direct fitness benefits to the apparent altruist (Griffin & West 2002). An interpretation of sentinel behaviour in birds (Bednekoff 1997), whereby time spent looking out for predators on behalf of others while not feeding oneself, had been seen in terms of mutualism. Under this model the energetic reserves or ‘state dependence’ of a sentinel is the key to this cooperative behaviour, with others gaining as a by-product from the sentinel’s ample energy reserves. The ‘state dependence’ model has also been supported by a study of sentinel behaviour in the Arabian babbler (*Turdoides squamiceps*) (Wright et al 2001).

The key point here is that these examples of apparent altruism or cooperation do not present a problem for Darwinian biology, as there is a mutual benefit to fitness for the individuals concerned. Although providing a valuable account of why certain forms of cooperation occur in nature, mutualism does not explain the core problem outlined at the start of this Chapter - altruistic behaviour where a reduction in fitness is voluntarily incurred by one individual resulting in a gain to the fitness of a non-relative.

1.9 Further Clarification of the Problem

1.9.1 Distinction between Altruism and Cooperation

Unfortunately workers from different disciplines often use the terms altruism and cooperation in quite different ways and, as a result, there has been confusion in the way the concepts have been defined (Noe 2006). Here, it is proposed that cooperation has a crucially different sense to the definition of altruism. The term ‘cooperation’ is seen as describing all interactions that, on average, result in a net gain in fitness for all participants compared with what is available to other individuals of the same species. So defined, this concept does not strictly represent a problem for natural selection and could be accounted for by various forms of mutualism. In contrast, the term ‘altruistic cooperation’ would denote only those interactions that result in a net loss to survival and/or reproductive success for the participants involved and a net gain for those helped. As such, 'altruistic cooperation' raises the same problem as that of altruism itself.

Similar confusion also arises in the use of the word 'altruism' itself. In common parlance, altruism has connotations of moral good. - a meaning certainly intended by Compte who invented the term - as discussed at the start of this thesis. However, the definition of altruism used in this thesis allows no such implication (i.e. 'any act that has the effect of increasing the chances of survival or reproductive success of another organism at the expense of that of the altruist'). Numerous examples of the morally dubious effects of altruistic behaviour are available in human history and so here altruism will be treated as a morally neutral concept.

1.10 Summary

- Examples of altruistic behaviour appear, at first sight, to be at odds with Darwin’s theory of evolution.
- The current consensus is that altruism towards non-kin is accounted for by reciprocity theory and later versions of it that rely on indirect reciprocity through reputation formation to enforce reciprocation. However, there has been no decisive breakthrough in empirical support for this body of theory.
- Asymmetry or inequality in power and status between individuals would appear to make reciprocation less likely and reputation formation less important. This point may be consistent with the rarity of evidence so far found in favour of direct or indirect reciprocity.
- Other models have been proposed to account for altruism towards non-kin but also lack substantial empirical support.
- By-product mutualism may account for certain examples of apparent altruism towards non-kin that actually result in a mutual benefit to fitness of those involved. Mutualism leaves the central problem of altruism unexplained – why individuals voluntarily reduce their fitness to promote the fitness of other non-kin.
- The problem of altruism towards non-kin is therefore not yet satisfactorily resolved.

CHAPTER 2: A LINK BETWEEN SEXUAL SELECTION AND HUMAN ALTRUISTIC TRAITS

2.1 Introduction

2.1.1 Altruism as a Sexually Selected Trait

In the previous chapter various theories put forward to resolve the puzzle of altruism towards non-kin were discussed. It was concluded that they lacked substantial empirical support despite the considerable amount of theoretical effort devoted to develop models to account for them. However, one particular theory was not discussed – and this will form the basis of Chapter 2.

Thirty years ago it was first proposed that altruism towards non-kin evolved as a way of providing a reliable signal of quality to others (Zahavi 1977). Specifically, it was suggested that altruistic behaviour was a 'handicap' that accurately indicated an individual's condition and viability. If the altruistic 'handicap' is successfully overcome, then this gives a reliable and 'honest' signal of superior genetic quality, reinforcing 'social prestige' and providing other fitness advantages (Zahavi 1977; Zahavi & Zahavi 1997). Subsequently, the 'handicap principle' became recognised as part of the 'indicator' sexual selection mechanism (Andersson 1994; Andersson & Simmons 2006). However, models that have explored Zahavi's concept of reliable or 'costly' signalling (e.g. Gintis et al 2001) have usually focussed on its wider effects – on same sex allies or competitors as well as potential other sex mates. A relatively small number of studies have considered a specific link between altruistic traits and sexual selection or reproductive competition (e.g. Kelly & Dunbar 2001; Leimar & Hammerstein 2001). But before discussing this idea further, the theory of sexual selection will be considered.

2.1.2 Darwin's Theory of Sexual Selection

Darwin (1859, 1871) recognised that certain traits regularly observed in nature such as song, bright colours, horns, and other weapons, appeared to reduce the chances of survival of those individuals displaying them. The existence of these traits therefore seemed to be at odds with his theory of natural selection. These traits also often appeared to be present in one sex but absent in the other. Darwin's solution was to recognise another selective process occurring in nature alongside natural selection – what he termed sexual selection. In contrast to natural selection Darwin saw sexual selection as depending:

> 'not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring.' (Darwin 1859).

Thus Darwin saw these apparently disadvantageous traits as bestowing an important selective advantage under reproductive competition that more than compensated for any selective disadvantages of these traits under natural selection. Darwin then went on to identify two distinct forms of sexual selection (Darwin 1871, p.614):

- Where there was aggressive competition, typically between males, to drive off or kill rivals with females remaining passive throughout. (This has since been called intrasexual selection);
- Where there is competition to attract mates (usually females) who then play an active role in selecting a mate. (This has since been termed intersexual selection).

Darwin also recognised the possibility of what he termed mutual sexual selection (Darwin 1871) or sexually selected traits being displayed in both sexes, although he did not clarify the conditions under which such a process might occur. He also identified examples of what he termed 'transference' of such traits (Darwin 1871, p. 241) to the other sex - the rudimentary horns of female reindeer being one example (Darwin 1871, p. 503-504).

2.1.3 History of Sexual Selection Theory

The theory of sexual selection met with strong resistance from Darwin's contemporaries and particularly from Wallace, the co-discoverer of natural selection (Cronin 1991). Most of the opposition centred on doubt that females could possibly exercise aesthetic choice in a way that resulted in the intricate ornamentation observed in males (Andersson & Bradbury 1987). After Darwin's death the theory was attacked by certain other leading authorities such a Morgan and Huxley (O'Donald 1980; Andersson 1994) whose views were influential in discrediting sexual selection as a theory among biologists of their time. As Cronin has put it:

‘for nearly a century, most of the work on sexual selection amounted to a concerted attempt to dispose of it entirely, and to rely on the more sober, utilitarian forces of ordinary natural selection to deal with Darwin’s splendid array.’ (Cronin 1991, p. 123).

Then attitudes began to change. Williams (1966) and O’Donald (1980) brought the attention of biologists to the earlier work of Fisher on sexual selection (Fisher 1915, 1958) while many field studies of animal behaviour (e.g. Semler 1971) began to find evidence of female choice of mates. Subsequently, a massive amount of empirical evidence became available that sexual selection favours secondary sexual traits in many species (Andersson 1994, p.130-142). This empirical evidence was backed up by genetic models that demonstrated the interaction between female choice and male preferred traits (e.g. O’Donald 1980; Lande 1981). After a century of rejection the theory of sexual selection became widely accepted among evolutionary biologists and has been seen as one of the fastest growing theories of modern biology (Andersson & Bradbury 1987).

Thus a large body of modern empirical and theoretical work has fully vindicated Darwin’s original vision (Andersson 1994). Here, I briefly review and summarise the vast literature, the aim being to demonstrate that sexual selection theory provides a sound basis upon which to make a link with the origin of altruistic behaviour towards non-kin.

2.2 Sex Roles in Relation to Mate Choice and Preferred Traits

2.2.1 Differing Strategies of Females and Males

One of Darwin's (1871) most basic observations about sexual selection was that it was usually females who exerted mate choice and males who competed to display the traits preferred by females. In more recent times a body of theory has been developed that attempts to understand why mate choice and preferred traits are typically expressed differently in each sex of a species.

Bateman's (1948) experiment on male and female breeding patterns in *Drosophila melanogaster* provided one answer. He found that male reproductive success varied much more widely than that of females and deduced that sexual selection was therefore occurring through intense male competition for reproductive access to females. Bateman inferred that female reproductive success, unlike that of males, was not limited by an ability to attract mates but by anisogamy or sex differences in gamete size. As eggs are more expensive to produce than sperm and therefore far fewer in number Bateman saw anisogamy as accounting for why females are the more choosy sex and why males are more likely to compete by displaying the preferred traits.

In another seminal article, Trivers (1972) put forward a further explanation, also discussed by Bateman (1948) and Williams 1966), for why females typically exert mate choice and males compete to display the traits preferred by females. He suggested that what ultimately governed the mating behaviour of each sex was the relative parental investment each made in its own offspring (Trivers 1972, 1985). Trivers defined parental investment as any investment made by a parent in one offspring that thereby limited the ability of that parent to produce further offspring. Recognising that the total number of offspring produced by each sex must be equal, Trivers concluded that individuals of the sex investing least (usually males) will compete more vigorously to attract the other sex since this is the only way they can enhance their reproductive success. As females are usually the sex that makes the heavier parental investment Trivers' theory is thus consistent with evidence of female mate choice and male reproductive competition.

Trivers (1972, 1985) was also able to show exceptions to the common pattern – that is, species where males make the larger parental investment and, unusually, females compete more intensely for mates. In these examples, including phalaropes and other polyandrous bird species, it is the females who court more vigorously, are larger than the males, are more brightly coloured and adopt more aggressive behaviour in mating competition (i.e. display the preferred traits seen in other species as typically male). Yet it is in precisely these species where, exceptionally, the females' parental investment ends when she lays her eggs and it is the males who brood the eggs and care for the offspring after hatching (Trivers 1972). Likewise, in pipefish and seahorses (*syngnathidae*) male parental investment is relatively high and correlates with female bright coloration and vigorous courtship (Trivers 1972). These 'exceptions that prove the rule' can thus be seen as giving powerful support to Trivers' theory. From this evidence it may be possible to infer that parental investment can outweigh anisogamy as the prime determinant of sex role, given that the same differences in egg and sperm size were presumably also present in these species.

A corollary of Trivers' (1972, 1985) theory of parental investment is therefore that where parental investment between the sexes is symmetrical (i.e. equal) there will be a corresponding similarity in degree of mate choice and display of preferred traits expressed by each sex. Trivers thus provided a ready means of testing his theory in the rare cases where mutual sexual selection is present.

Other models have since been put forward that give alternative accounts of why different sex roles occur. Emlen & Oring (1977) suggested that the intensity of competition under sexual selection was determined by the operational sex ratio (OSR). This was defined as the average ratio of sexually receptive males to females at any given time, making allowance for time needed to recover from a particular breeding attempt. Difficulty in measuring OSR directly (Clutton-Brock & Vincent 1991; Kokko & Monaghan 2001) then led to the suggestion that the potential reproductive rate (PRR) of males and females was a more easily measured predictor of choosiness and reproductive competition between the sexes (Clutton-Brock & Vincent 1991). Thus the higher potential rate of reproduction (measured as the maximum number of offspring that parents can produce per unit time) of males was seen as explaining why mating competition among males was more intense.

Subsequently, Kokko & Monaghan (2001) developed a model that predicted sex role by taking account of parental investment, mortality, sex ratio at maturation and quality variation between the two sexes. Of all these factors, they saw the cost of a single breeding attempt as having the strongest direct effect on mate competition and choosiness in each sex. This work was extended by Kokko & Johnstone (2002) who used a game theoretical model to examine Kokko and Monaghan's (2001) results.

They concluded that parental investment was the primary determinant of sex roles as opposed to OSR. Wade & Shuster (2002) also modelled the evolution of male parental care and established the circumstances under which paternal care of offspring can over-ride gains to the male under reproductive competition.

Another view was provided by sexual conflict theory (Arnqvist & Rowe 2005). Here, the suggestion was made that the sexes often conflict over reproductive decisions since each mate has different interests. This leads to sexually antagonistic co-evolution which was seen as underlying the different sex roles reflected in mate choice and reproductive competition. Games theory modelling (Parker 1979) and genetic modelling (Gavrilets et al 2001) has helped to explore this perspective.

Finally, Simmons and Kvarnemo (2006), making use of Kokko & Monaghan's (2001) model, have proposed that the cost of breeding is the single most important factor that predicts a mating system. This was defined as the probability of dying as a consequence of the current breeding attempt, including the 'time out ' required to undergo and recover from a breeding attempt.

2.2.2 Commentary on How Sex Roles Evolved

I see theoretical and empirical work on what determines which sex exercises mate choice and which displays the preferred traits as being dogged by overlapping concepts, probably based on difficulty in measuring the determinants involved. For example, Trivers' (1972) concept of parental investment appears to accord closely with what operational sex ratio (OSR) (Emlen & Oring 1977) and the mortality cost of a breeding attempt (Simmons & Kvarnemo 2006) are also concerned with (i.e. constraints imposed by the cost of parental investment). It is also difficult to see how potential reproductive rate (PRR) (Clutton-Brock & Vincent 1991) could not be, in some way, a function of parental investment or why sexual conflict is not bound to be at least partly a consequence of differing levels of parental investment. Perhaps the desire by workers to claim a 'new' theory has detracted from efforts to consolidate and simplify understanding of existing theory and empirical evidence. The problem of measuring parental investment is best illustrated by Knapton (1984) who proposed that it takes three distinctively different forms - time, energy and risk. As these three forms are not additive (Knapton 1984), accurate measurement of total lifetime parental investment becomes problematic, if not impossible.

2.3 How Is Mate Choice Made?

2.3.1 Introduction

Given that mate choice is fundamental to intersexual selection, the next question is – on what basis is such mate choice made? As discussed above, an early objection to sexual selection theory was that the females of a species could not possibly be capable of exercising the discrimination necessary to favour the often complex patterns found in sexually selected characteristics in many species. However, a number of mechanisms have since been proposed to account for how females arrive at a mate choice (Andersson 1994; Andersson & Simmons 2006) and these are reviewed below.

2.3.2 Fisher's 'Runaway' Process

An early approach to understanding how mate choice drives the evolution of sexual selection was proposed by Fisher (1915, 1958). He envisaged a self-reinforcing inter-relationship developing between genes coding for a mate preference in females and a preferred trait in males. Under this genetic feedback loop, growth in preference and trait would increase at an exponential rate, hence the term 'runaway' selection. The process would only be brought to a halt by the ever-increasing cost of the preferred trait under natural selection – and, indirectly, the mate preference.

The traits being favoured by such a process Fisher saw as quite arbitrary and not related to improving the survivability of the individuals displaying them. The elaborate tail feathers of peacocks are often used as the classic example of 'runaway' selection. At some point the cost to survivability of the peacock's tail feathers in terms of marginal extra energy cost and vulnerability to predators was seen as preventing further increase in the size and complexity of this trait.

In his early formulation of this theory Fisher (1915) made it clear that 'runaway' selection could have had a particularly important impact on human evolution. Fisher discussed both human 'beauty' and the 'principles of right' or 'morality' 'that governs our motives and guides our actions' (Fisher 1915) as possibly influenced by 'runaway' selection. Thus Fisher speculated that these human traits, which could possibly be seen as akin to altruism, might have evolved as a result of this process.

Fisher’s argument ran so contrary to the consensus in biology that it was largely ignored until the 1960s (Andersson & Bradley 1987). Then a series of studies by O’Donald (reviewed in O’Donald 1980), using a two locus diploid model, provided a mathematical basis for Fisher’s verbal outline. O’Donald found that the most rapid selection would occur where the preferred trait is rare and that a recessive allele would be selected faster than a dominant one (O’Donald 1980). Kirkpatrick’s (1982) haploid two-locus model also helped to clarify the dynamics of the evolution of mate preference and preferred traits.

It is more realistic to see mate preference and preferred trait as dependent on alleles at many different loci (Andersson 1994) and thus quantitative genetic models offer a more accurate means of testing ‘runaway’ sexual selection. Lande (1981, 1987) was the first to model selection using this approach. He assumed a polygynous mating system with males providing no resources other than genes and additive genetic variability being continually replenished by mutation. Lande was thus able to demonstrate a sound mathematical and genetic basis for Fisher’s original verbal outline.

2.3.3 Indicator Mechanisms

Fisher’s (1915) article on the evolution of mate preference was also the source of another approach to understanding the basis upon which sexual selection works. In discussing how the link between mate preference and preferred trait could get started Fisher speculated that the trait might ‘only derive its importance from being associated with the general vigour and fitness of which it affords a rough index’

(Fisher 1915). Thus if a well developed trait indicates good condition and genetic quality then a female selecting a male with such a trait will ensure that her offspring inherit superior genetic quality from their father.

A number of indicator or ‘good genes’ models have been proposed of which probably the best known is Zahavi’s ‘handicap principle’ (Zahavi 1975, Zahavi & Zahavi 1997). Zahavi’s starting point was that any trait that indicates phenotypic or genotypic quality must provide an accurate and ‘honest’ signal of what it claims to reveal or else it is worthless to those attempting to use it to select mates. Darwin and Fisher had seen sexually selected traits that handicapped their owners merely as a by-product of sexual selection. Instead, Zahavi suggested that their very cost to the survival chances of the individual bearing them were what provided an ‘honest’ and accurate signal of underlying genetic and phenotypic quality to potential mates – and, therefore, was precisely the point of the process. Although an individual with a high quality genotype would in an obvious sense be better off without the handicap, that individual would be still worse off in the sense that potential mates would not be able to recognise that individual’s superior genetic quality (Zahavi 2003). Later, Zahavi (2003) clarified a misunderstanding of his earlier work by making it clear that successful signallers increase their net fitness by displaying their handicap and that it was only ‘cheats’ who decreased their fitness by displaying a handicap that did not match their phenotypic or genetic quality.

Zahavi’s handicap principle provoked much interest of a sceptical kind when it was first put forward, in part perhaps because of the apparently counter-intuitive nature of the theory itself. It was not until a mathematical model was able to satisfactorily demonstrate its feasibility (Grafen 1990, a, b) that it gained a secure acceptance as part of sexual selection theory.

Nevertheless a difficulty with indicator models was seen to be that if mate choice is based on genetic quality it is likely to quickly exhaust genetic variation in a population - with the result that no one mate will be better off in using these indicators of ‘good genes’ - the so-called ‘lek paradox’ (Hamilton & Zuk 1982; Kirkpatrick & Ryan 1991). In fact, additive genetic variation in sexually selected traits has been measured in wild populations and found to be actually greater than in other traits (Pomiankowski & Moller 1995; Gangestad & Simpson 2000; Amqvist & Rowe 2005). How can this evidence be consistent with the operation of indicator mechanisms – or, indeed, other sexual selection models? One solution to this difficulty was proposed by Hamilton and Zuk (1982) who pointed to the fact that organisms in nature are often under constant attack from parasites and pathogens. Thus successful resistance to the ever-changing genetic structure of these parasites and pathogens may become an important indicator of ‘good genes’ in choosing a mate. This could therefore result in sexual selection actually promoting genetic variation rather than exhausting it.

Hamilton and Zuk’s model has been supported by reviews of studies of North American birds (Hamilton & Zuk 1982 though see Kirkpatrick & Ryan 1991) and a range of other species (Andersson 1994). Nevertheless, as Lande (1987) has pointed out, if the primary function of sexually selected traits is to reveal freedom from parasites and pathogens then it would seem sufficient for closely related species to share one or a few types of such traits. Instead, as Darwin observed, closely related species often differ most in secondary sexual traits which would therefore appear to be inconsistent with this suggested function (Lande 1987).

2.3.4 Direct Benefits or Phenotypic Effects Mechanism

Another approach to accounting for how mate choice works envisages selection acting directly on the mate preference through direct benefits or phenotypic effects accruing to the female and her offspring as a result of her mate choice. This may apply, for example, where traits reduce the mate search costs of the female or help her to assess the quality of the material benefits a potential mate can offer (Kirkpatrick & Ryan 1991; Ryan 1998). Factors involved here include the material contribution that a male can make to the fecundity and viability of the female through the provision of ample food resources, the quality of male parental care of offspring, whether sufficient sperm is made available to fertilise the female's eggs and the adequacy of protection against predation and attack by conspecifics.

Mate preference may take more indirect forms – that is, the female is selecting a trait that is an index of possession of the desired resources – and where this applies could even be classed as another form of indicator mechanism (Andersson 1994). The quality of territory held or the position of the mate in any dominance hierarchy may well correlate with possession of various direct benefits. It is also possible that, while the female mate preference is genetically determined, male variation in the desired traits may be influenced entirely by environmental factors (Andersson 1994; Amqvist & Rowe 2005) and some models have been developed on this basis (Heywood 1989; Hoelzer 1989).

2.3.5 Sensory Bias Mechanism

A mate preference might evolve as a consequence of a pre-existing bias in the sensory system of a species (Endler & Basolo 1998; Ryan 1998; Boughman 2002). For example, the peacock's tail feathers with its many 'eye-spots' might get the attention of females by exploiting a widespread responsiveness to eyes in animal cognition (Andersson 1994). Thus the preference could initially evolve under natural selection but be exploited by males who then become favoured by the evolving mate choice under sexual selection (Andersson & Simmons 2006). Numerous models, based on slightly different versions of this principle, have been proposed (Endler & Basolo 1998).

2.3.6 Genetic Compatibility Mechanism

There may be selective advantages not only in choosing 'good genes' under an indicator mechanism but also in choosing genes that complement those of the individual who makes the mate choice (Trivers 1972; Mays & Hill 2004).

2.3.7 Conclusion on Sexual Selection Mechanisms

What these sexual selection mechanisms have in common is the notion of a mate preference expressed in one sex favouring a preferred trait displayed in the other. It may be wise not to see these mechanisms as mutually exclusive (Kokko et al 2003) but instead to treat the evolution of mate preferences as likely to be influenced by more than one mechanism (Andersson & Simmons 2006). It is also possible that, at various stages in the evolution of a sexually selected trait, different mechanisms made different impacts. For example, a trait may have evolved initially under the 'runaway' process but at a later evolutionary stage may have developed as a reliable indicator of freedom from parasite infestation (Kirkpatrick & Ryan 1991). Darwin's theory of sexual selection (Darwin 1871) is thus underpinned by an abundance of theory and mathematical modelling which provides a sound basis upon which to proceed with assessing a possible link between sexual selection and altruistic traits.

2.4 Empirical Evidence in Favour of Sexual Selection Theory

2.4.1 Overview of Literature

What empirical evidence is available to support the theoretical foundation for sexual selection? Numerous studies have found statistically significant relationships between mating success and sexually selected traits in field observations, experiments and laboratory work (Andersson 1994). Here, some of the leading empirical studies are briefly reviewed including those particularly pertinent to this thesis.

Evidence of female mate preference towards traits that offer no obvious phenotypic benefits was provided by Semler (1971), Andersson (1982) and Hoglund et al (1990). Red nuptial coloration in male threespine sticklebacks *(Gasterosteus aculeatus*) (Semler 1971) is widespread across populations of this species, a character thought to make them more vulnerable to predation by trout. Approximately 14 % of breeding males in Semler's study developed red coloration and in a series of mate preference tests females demonstrated a significantly greater tendency to mate with such males. Semler however found that red coloration reduced territorial intrusion by other males intent on egg predation so a link with intrasexual selection could not be ruled out. In contrast, elongated tail length in widowbirds

(Euplectes progne) appears not to be associated with either quality of territory or intrasexual competition between male birds (Andersson 1982). In this African genus of polygynous weaverbirds males provide no parental investment. Yet when the tails of certain males were artificially elongated it was observed that they enjoyed greater mating success while those with artificially shortened tails experienced the least mating success. A similar study of a lek-breeding bird - the great snipe *(Gallinago media*) - where the white area in the tail feathers of a male bird was experimentally enlarged came to a similar conclusion (Hoglund et al 1990). Resources or quality of territory could not account for female mate preference towards an experimentally enlarged white while area in the tail feathers of the male bird.

Mate preference in these three studies could be interpreted as consistent with either the 'runaway' or indicator mechanisms, as discussed above. An interpretation more clearly in favour of the 'runaway' mechanism as made by Brooks 2000) in another study of guppies *(Poecilia reticulata*). Here, male traits enhancing sexual attractiveness were found to have a negative genetic correlation with both offspring survival and the number of sons maturing, a result interpreted as consistent with Fisher's prediction that the fitness costs of ornamentation will evolve to balance the benefits under attractiveness.

The first study that claimed to demonstrate a correlation between female mate preference and both female fecundity and male viability involved spur length in male pheasants *(Phasianus colchicus*) (von Schantz et al 1989). It could thus be claimed as supporting the indicator mechanism with spur length acting as an accurate index of ‘good genes’ in this species (Kirkpatrick 1989). The effects of intrasexual selection and territorial quality were seen as unlikely to have influenced the result.

An advance in understanding the genetic mechanism by which a mate preference is inherited was offered by a study of the moth *Utetheisa ornatrix* (Iyengar et al 2002). In this species females mate preferentially with larger males, receiving both direct phenotypic and indirect genetic benefits in doing so. The authors were able to show that daughters inherit this mate preference directly from one of their father’s sex chromosomes. Mate preference and preferred trait were found to be correlated, with those females who had larger fathers displaying a stronger mate preference towards larger males.

Correlation between mate choice and preferred trait is central to understanding how sexual selection works and so demonstrating such a relationship empirically was a key step forward. In a study of guppies *(Poecilia reticulata*) (Houde & Endler 1990) female mate choice was found to favour conspicuous orange patterns in males with populations differing significantly in the degree of female mate preference for this trait. Houde and Endler (1990) were able to demonstrate that, across seven populations, the degree of female mate preference was correlated with the population average size for the orange area. They thus concluded that female mate preference and male trait appeared to be evolving in parallel. In stalk-eyed flies *(Cyrtodiopsis dalmani*) (Wilkinson & Reillo 1994) males exhibit pronounced sexual dimorphism in eye span length with females apparently choosing males on the basis of longer eye span. In this study (Wilkinson & Reillo 1994) populations taken from the wild were subjected to artificial selection in a laboratory with lines of longer and shorter eye span being selected. After 13 generations of this bi-directional selection females from longer eye span lines were found to prefer males with longer eye span and females from shorter-eyed lines preferred males with shorter eye spans. No evidence was found that mate choice impaired female survival or fecundity.

Species where both sexes provide parental investment provide an opportunity to test the basis of how sex roles evolve. Both sexes of the crested awklet *(Aethia cristatella*) are thought to contribute similar amounts of parental investment (Jones & Hunter 1993), while both display spectacular forehead crest feathers during the breeding season. Three male and three female models with crest feathers shortened or lengthened were placed in a position to observe responses. Overall, the results demonstrated a strong relationship between larger crest size and sexual attractiveness in both sexes. Empirical evidence of both sexes expressing mate choice and preferred trait in a species where both make symmetrical parental investment is thus consistent with Trivers' (1972, 1985) prediction, as discussed above.

The ability to discriminate in mate choice through odour has been demonstrated in various non-human species but two studies of human mate preference (Ober et al 1997, Jacob et al 2002) have demonstrated that females can also use odour to discriminate in mate choice. Female mate preference for male odour has been traced to HLA (human leukocyte antigen) alleles which are inherited paternally (Jacob et al 2002) while a mate preference that leads to avoidance of spouses with HLA haplotypes that are the same as one's own has also been demonstrated (Ober et al 1997). This could be seen as an example of the genetic compatibility mechanism.

2.4.2 Empirical Evidence: Conclusion

Abundant evidence thus confirms that sexual selection theory has a sound empirical basis. The examples here also illustrate that sexual selection applies to species with widely different characteristics and can take many widely different forms. Evidence for a genetic correlation between mate choice and preferred trait has been demonstrated and the genetic mechanism underlying certain mate preferences elucidated. While no conclusive test of any single sexual selection mechanism is yet available (Andersson 1994; Andersson & Simmons 2006) there is nevertheless evidence that can be seen as consistent with certain mechanisms.

2.5 Sexual Selection and Human Evolution

2.5.1 Are Humans a Sexually Selected Species?

In *'The Descent of Man'* Darwin claimed that sexual selection 'appears to have acted powerfully on man' (Darwin 1871, p.198) and he pointed to many distinctively human characteristics such as singing and oratory (Darwin 1871, p. 572), beauty (Darwin 1871, p.573) and the relative lack of human body hair (Darwin 1871, p. 600) as likely consequences of sexual selection. He also saw sexual selection as accounting for racial differences between humans (Andersson 1994; Moore & Desmond 2004), rather than the more obvious explanation of adaptation to climate. Darwin made similar claims for supposed differences between the sexes.

Darwin's view that sexual selection played a major part in the evolution of humans has been taken up in modern times by Miller (2000) who has suggested that the human mind and the peacock's tail may serve similar biological functions. In his book, *The Mating Mind*, Miller questioned whether the range of sophisticated human attributes including, for example, language, art and morality could have enhanced the survivability of early humans and therefore could have evolved entirely on the basis of natural selection (Miller 2000, p. 2). Instead, he suggested that with the evolution of language 'thought itself became subject to sexual selection' (Miller 2000, p. 10). Miller envisaged the evolution of human intelligence and many other distinctively human characteristics in terms of there serving as indicators of 'good genes' under sexual selection.

My concern with Miller's case is that he offers no critical test with which his hypothesis might be tested and makes strong claims without a firm foundation of empirical evidence to support it. Science advances not only by bold and sweeping speculations but also by patient and rigorous testing of hypotheses. There is, however, one example of where Miller's case has been tested empirically, albeit in another species. In his book, *The Mating Mind,* Miller drew a parallel between sexual selection in humans and bowerbirds (Miller 2000, p. 267-270). In this family (*Ptilonorhynchidae*) male bowerbirds construct bowers to attract mates – a task that requires a degree of behavioural complexity with the more elaborately constructed bowers often resulting in their owners enjoying greater reproductive success (Madden 2001). Thus in selecting the most impressive bower, the female is also indirectly selecting for greater behavioural complexity - and presumably also greater intelligence. Madden carried out an analysis of brain size in bowerbirds and closely related species that did not build bowers. He also measured the brain size of distantly related species that did not build bowers but lived in a very similar environment to bowerbirds to establish whether any confounding environmental variables may have been present. Madden found that species that did build bowers had larger brains than those who did not, thus suggesting an indirect relationship between sexual selection and brain expansion. He also found evidence of greater brain size in female bowerbirds, presumably as a result of 'transference' of the trait from the male (Darwin 1871, p. 241). Madden then felt able to interpret his findings as giving support to Miller's suggestion of a connection between sexual selection and brain expansion during human evolution (Madden 2001).

Miller (2000) argued that the environment of the Pleistocene epoch would have offered little obvious selective challenge that could credibly account for the rich diversity of human intellectual skills and behavioural traits. On the other hand, human intellectual abilities may have evolved in a form of feedback loop in which the need for increasing sophistication in the use of tools for hunting and butchering carcasses created increasing selective challenges that, in turn, would have led to increasing brain size. This suggestion is, however, contradicted by evidence that the periods of substantial increase in hominid brain size do not coincide with any marked increase in complexity of tool design (Leakey & Lewin 1981, p. 155-156; Maynard Smith & Szathmary (1997) or environmental complexity (Blumenberg 1983).

Another proposal is that, as primates are typically social species, the selective challenge of coping successfully with numerous interactions between individuals in groups would have favoured increasing intelligence and therefore expanding brain size (Dunbar 1992). This hypothesis is supported by evidence for a positive relationship between group size and neocortex ratio in primates (Dunbar 1992, Dunbar 2003). It is suggested that, in hominids, language may have evolved to bridge the gap between the time they would have had to spend on social interactions and the limited time available as a result of other selective pressures (Dunbar 2003).

One telling point in favour of sexual selection having acted powerfully on humans was not mentioned by Miller (except obliquely: see Miller 2000, p.169). This point lies in Darwin's observation that (a) closely related species differ most in their sexually selected traits (Darwin 1871; Boughman 2002). From this observation it follows that (b) sexually selected traits are among the most rapidly evolving of all traits found in nature (Carson & Lande 1984; Lande 1987; Eberhard 1993). Yet (c) recent estimation of the split between the human and chimpanzee lines indicates that it occurred less than 6.3 million years ago or probably less (Patterson et al 2006). In evolutionary terms, this can be seen as a relatively short period. It therefore follows that (d) all the distinctive characteristics that make humans different from chimpanzees must have evolved at a relatively rapid rate in evolutionary terms. The logical conclusion is therefore that (e) the origin of such distinctively human traits is consistent with it being influenced by sexual selection.

This speculation is no doubt one of many that could, equally plausibly, account for what occurred in human evolution. It requires further development before testing – for which there is insufficient space here. The point of mentioning it is that if human altruism towards non-kin is seen as taking a unique form (Fehr & Fischbacher 2003) then this logic is consistent with it also having had a sexually selected origin.

2.5.2 Human Altruistic Traits and Sexual Selection Mechanisms

How consistent might the sexual selection mechanisms discussed above be with the notion of human altruism as a sexually selected trait? Firstly, this notion can be seen consistent with the ‘runaway’ mechanism in that while altruism clearly involves a selective disadvantage it could also have been seen as an attractive trait that early humans might increasingly have had to display in order to mate successfully. It is also plausible to view human altruism as a ‘handicap’ that, if successfully overcome, for example in selfless defence of a group from attack by predators or conspecifics, might thereby have accurately revealed superior genetic quality. It could also have been linked to the direct phenotypic benefits mechanism where selfless behaviour prior to mating is correlated with a subsequent commitment to provide resources and protection to a female and her offspring after mating. Under the sensory bias mechanism it is possible that altruistic behaviour towards close relatives (Hamilton 1963) might have created a sensory bias in females that could then have been exploited by hominid males in displays of altruism towards non-kin. Finally, where the social environment offered selective advantages to exhibit both selfish and altruistic genes in different contexts it may have been beneficial for offspring to carry genes associated with both strategies, thus promoting genetic compatibility.

I conclude that there are good grounds for supposing that human altruism might have been implicated in hominid sexual selection. The principle aim of this thesis will therefore be to test the hypothesis that human altruism towards non-kin evolved as a result of sexual selection.

2.6 Sexual Selection and Human Altruistic Traits

2.6.1 Links Made between Sexual Selection and Altruistic Traits

Zahavi was the first to propose, under his ‘handicap principle’, that a signal is reliable when the difficulty of its performance is related to its quantity and quality (Zahavi 1975, 1977). He then proposed that altruistic traits provide ‘honest’ signals of genetic and phenotypic quality to others (Zahavi 1977). As long as the altruist is able to overcome the reduction in viability resulting from the handicap more successfully than competitors, the altruist is able to reap the reward of enhanced reproductive success.

The connection between the ‘handicap principle’ and altruism was suggested by Zahavi’s study of Arabian Babblers (*Turdoides squamiceps*), a group-breeding songbird. Noting that reproductive success increases with social rank (Carlisle & Zahavi 1986), Zahavi found that apparently altruistic traits such as food donation and sentinel behaviour denoted high status to other group members (Zahavi 1977, 1990, 1995; Carlisle & Zahavi 1986; Zahavi & Zahavi 1997). Food donation, for example, was almost always made by individuals dominant to the recipient and if the gift was refused this provoked aggression from the dominant bird (Carlisle & Zahavi 1986). He found other examples of apparent competition in making altruistic displays – behaviour that could not readily be explained by reciprocity or other theory – and even drew parallels with the human custom of competitive gift-giving or ‘potlatch’ observed among Amerindians (Zahavi 1990). The altruistic behaviour that denoted high status he saw as carrying a handicap that revealed the underlying genetic and phenotypic quality of the altruistic individual to those who observed it. In terms of reproductive competition, Zahavi argued that the cost of altruism was no different from the cost of the peacock's tail feathers or any other sexually selected trait (Zahavi & Zahavi 1997). He concluded that this explanation of altruistic behaviour:

> 'holds true not only for babblers and other birds, but also for mammals, including humans, for social insects, and even for one-celled organisms.' (Zahavi & Zahavi 1997, p.150).

Others (Boone 1998; Roberts 1998; Kelly & Dunbar 2001; Leimar & Hammerstein 2001) have also considered the notion of a link between the 'handicap principle' and the evolution of altruistic traits. Gintis et al (2001) have developed a game theory model in which cooperation in the provision of a public good is seen as giving a 'costly signal' to others of individual quality. But it should be made clear that their study is concerned as much about coalitions with same sex allies and against same sex competitors as it is with mate choice and therefore is not solely concerned with sexual selection. In this thesis, it is suggested that mate choice is likely to exert a far more direct and powerful effect on individual fitness than coalition formation with same sex others, although it is difficult to see how this assumption could be tested (see discussion in Section 8.6).

Gintis et al's (2001) model has been supported by a number of empirical studies. One study found that individuals often pursue relatively inefficient hunting or sharing choices in ways that were seen as giving an 'honest signal' of the hunter's qualities to observers (Bliege Bird et al 2001). Another study (Farthing 2005) found mate preference towards 'heroic physical risk takers' was present in both sexes and concluded that it could be a form of ‘costly signalling’ directed towards both female and male peers. Milinski et al. (2002) conducted a study of donations made in public to a relief organisation that resulted in enhanced reputation and other benefits to the donors as a result of this signal of social reliability.

A specific connection between sexual selection and altruism has been discussed by Tessman (1995) and by Cronin (1991) who speculated that Darwin might also have linked the large human brain with our moral sense and sexual selection:

‘Perhaps, then, he saw our moral qualities as one of the peacocks’ tails that flourish in our mental world, the result of selective pressures to which there is no natural end. If so, Darwinians should not be alarmed at the vast gulf that morality puts between us and the ‘lower animals’.’ (Cronin 1991, p. 349-350).

As discussed above, Miller (2000) has proposed that altruistic traits evolved as indicators of ‘good genes’ under sexual selection, suggesting that:

‘We have the capacity for moral behaviour and moral judgements today because our ancestors favoured sexual partners who were kind, generous, helpful, and fair.’ (Miller 2000, p.292)

He continued:

‘As with most reliable fitness indicators, the point of moral displays is not so much the benefit conferred on others, but the cost imposed on oneself. Morality is a system of sexually selected handicaps – costly indicators that advertise our moral character.' (Miller 2000, p. 294).

2.6.2 Reproductive Success and Traits Allied to Human Altruism

Before considering the proposed link between sexual selection and altruism empirical studies that have focussed on traits analogous to altruism towards non-kin will be reviewed. Buss & Barnes (1986) found 'considerate', 'honest', 'affectionate' 'dependable' 'kind' and understanding' among the ten most valued characteristics in a mate (out of 76 characteristics) in a sample of spouses. Furthermore, females were found to prefer all of these characteristics significantly more than males (Buss & Barnes 1986). Employing principal components analysis on their data, they demonstrated that 'kind-considerate' had the highest factor loading of the nine interpretable factors found. In a separate sample, Buss & Barnes found 'kind and understanding' ranked as the top most desirable characteristic by both sexes (out of 13 characteristics) although no significant sex difference was found. This result was replicated in a much larger international study (n = 9,474) (Buss et al 1990). The question as to what extent these traits are analogous with the definition of altruism used in this thesis (i.e. 'any act that has the effect of increasing the chances of survival or reproductive success of another organism at the expense of that of the altruist') has then to be asked. It could well be that displays of altruistic behaviour towards non-kin may have provided 'honest' cues to potential mates of the very qualities rated so highly in this study.

In another study Howard et al (1987) defined ‘expressive’ as ‘affectionate, compassionate, expresses tender feelings easily, and romantic’ (Howard et al 1987). They found significantly greater female mate preference towards ‘expressive’ mates among both heterosexual and homosexual couples (Howard et al 1987) and that preference for ‘expressive’ mates positively correlated with relationship satisfaction.

Jensen-Campbell et al (1995) explored the hypothesis that there is a female attraction towards displays of ‘pro-social orientation’ in males, which they associated closely with altruism. In three multi-method studies they were able to produce evidence consistent with this hypothesis.

Kelly & Dunbar (2001) conducted a study that examined a link between human sexual selection and altruism, bravery and heroism, but also considered other relationships. Noting how nonadaptive these behaviours were in terms of natural selection, Kelly & Dunbar analysed female preference towards these characteristics in short-term partners, long-term partners and male friends. Profiles of eight males were presented to subjects, which reflected ‘brave’, and ‘altruistic’ personality traits and their opposites. Whether the role was carried out on a voluntary basis or as part of a paid job was also specified. These profiles were presented to female subjects who were then asked to rate each profile in terms of its attractiveness on a 5 point Likert-type scale. A matching sample of male subjects was included to test how aware they were of female preferences portrayed in the eight profiles.

The study found that females preferred brave males to non-brave males and that males were aware of this preference. However, brave, risk-prone men were less highly rated as long-term partners than as short-term liaisons or friends, perhaps reflecting a disinclination to mate with and be supported by men who may suffer higher mortality (Kelly & Dunbar 2001). ‘Altruism’ however played a lesser part in female choice. Females preferred ‘altruists’ as long-term partners and friends but ‘non-altruists’ as short-term partners (Kelly & Dunbar 2001). Kelly and Dunbar concluded that heroism might well have evolved due to female mate preference and that risk-taking acts could have acted as an honest cue for ‘good genes’ in a potential mate.

2.6.3 Possible Evidence of a Link between Altruism and Sexual Selection from the Anthropological Literature

Humans are seen as having evolved in hunter/gatherer societies and therefore this social environment is important in understanding the possible origins of human altruism towards non-kin. Anthropological studies of modern hunter/gatherer societies, in so far as they accurately reflect what occurred in ancestral populations (Landers 1994), may thus provide important insights into this question. Such studies have found sharing of hunted meat among non-kin common in such societies and this behaviour may thus be among the earliest forms of altruistic activity among non-kin with which humans were involved.

Studies by Kaplan & Hill (1985) and Hawkes (1991, 1993) have found that there was little, if any, relationship in modern hunter/gatherer societies between the amount of large and medium-sized game acquired by hunters and how much of it they and their families actually consumed. Hawkes found considerable variation in success in providing hunted meat to the group and that this variability in providing such a 'public good' could not be attributed to greater skill alone since more successful hunters were also found to spend a larger amount of time hunting (Hawkes 1991; 1993).

In these anthropological studies the word 'altruistic' was not used to describe the behaviour of successful hunters. However, their behaviour conforms with the definition of altruism used in this thesis (any act that increases the chances of survival and reproductive success of another individual at the expense of that of the altruist). These hunters could have:

- Adopted another strategy for food acquisition more likely to benefit themselves and their family (Hawkes 1993);
- Withheld their hunting activity until other hunters reciprocated the provision of hunted meat;
- Demanded a greater share of hunted meat to match their contribution.

Their hunting activity is likely to have required more energy expenditure than that of less successful hunters and probably involved greater risk of injury and death from the animals they hunt (Kaplan et al 2000). Less successful hunters could thus be seen as pursuing a 'selfish' and apparently 'fitter' strategy likely to be favoured by natural selection.

Hawkes (1993) asked why some hunters target resources that will go mostly to others and saw the answer in terms of 'favourable attention' received from other members of the group:

‘Advantages may include deference in decisions about travel, support in disputes (or at least reluctance on the part of others to side against them), and enhanced mating opportunities.’ (Hawkes 1993)

In mentioning this third point Hawkes has highlighted a major finding of anthropological studies. More successful hunters, and by implication here more altruistic individuals, enjoyed greater reproductive access to females (Hawkes et al 1985; Kaplan & Hill 1985; Hill & Kaplan 1988; Hawkes 1991; Hill & Hurtado 1996; Smith 2004). What is equally important is that the offspring of these more successful hunters were also found to have higher survivorship rates (Kaplan & Hill 1985; Hill & Kaplan 1988; Hawkes 1991; Hill & Hurtado 1996). This last finding is consistent with successful hunting activity (and by implication here altruistic behaviour) being seen as a handicap voluntarily undergone to successfully provide an ‘honest’ signal of superior quality to potential mates (Zahavi 1977, 1995; Zahavi & Zahavi 1997). This is evidenced not only in enhanced reproductive success but also in the higher survivorship rate of the resulting offspring. This evidence is also consistent with Fisher’s ‘runaway’ selection (Fisher 1958) and with the ‘direct benefits’ mechanism (Kirkpatrick & Ryan 1991) as long as mating with successful hunters produced an indirect benefit to the female and her offspring through her gaining nutritional benefits that might otherwise be lost if the hunter went elsewhere.

2.7 Scenario in which Human Altruism towards Non-Kin might have been Favoured

2.7.1 Increase in Level of Parental Investment as a Result of the Expanding Human Brain

At this point it is relevant to ask whether any particular distinctive conditions in human evolution might have contributed to the evolution of altruistic traits. One condition is likely to have been the increasing size of the human brain and a consequent increase in total parental investment needed to successfully raise human offspring to reproductive maturity.

Firstly, the increased size of the prenatal brain has been seen as leading to ‘premature’ birth in relation to human lifespan in order to help mother and offspring to survive parturition (Portmann 1990). It has been calculated that for human newborns to be as developed as other mammals at birth human gestation should last twenty-one months as opposed to nine months (Portmann 1990, p.51). One result of this evolutionary shift to relatively ‘premature’ birth would have been that human newborns were far more helpless than those of other mammals – so-called ‘secondary altriciality’ (Portmann 1990) - and thus would have required an extended period of dependence on parental care.

Secondly, it has been estimated that the average human brain is some 4.6 times larger than that expected for an average mammal (Aiello & Wheeler 1995). As the brain is expensive in terms of energy consumed one would therefore expect that the energy cost of the human body to be higher. The basal metabolic rate (BMR) is an index of this cost but the human BMR has not been found to be much different from that of other species (Aiello and Wheeler 1995). Aiello and Wheeler (1995) account for this by providing data suggesting that the increase in mass of the human brain was balanced by a corresponding reduction in the size of the gastrointestinal tract – the so-called ‘expensive tissue’ hypothesis (Aiello and Wheeler 1995). An important consequence of this evolutionary shift would have been that a high quality diet was essential to compensate for the smaller gut size (Aiello & Wheeler 1995; Aiello et al. 2001). This inference is supported by evidence that humans in modern hunter-gatherer societies consume far larger amounts of high quality but difficult to extract resources, such as animal protein, than closely related primates (Gangestad 2007).

These two key evolutionary shifts – the longer period of offspring vulnerability and the necessity for a high quality diet – would have increased the total parental investment in offspring required to successfully raise them to reproductive maturity. Trivers (1972) defines parental investment by reference to its negative effect on the parent’s ability to invest in other offspring. These shifts towards greater total parental investment per individual offspring are thus likely to have substantially reduced the potential lifetime number of offspring a hominid female would have been able to raise to reproductive maturity without extensive provisioning and protection by others.

2.7.2 Possible Responses

The ‘grandmother hypothesis’ (Hawkes et al 1998) offers one response to this predicament. The duration and size of parental investment required of hominid mothers could have selected against giving birth beyond a certain age – hence the menopause. Instead, this would have enabled grandmothers to improve their fitness by investing resources in their daughters’ reproductive success. There is empirical evidence that such a strategy does improve the viability of offspring, although the data relate to agricultural rather than hunter/gatherer societies (Lahdenpera et al 2004).

Another evolutionary response to the increasing cost of raising offspring to reproductive maturity would have been for hominid males to make a correspondingly greater parental investment. In modern hunter/gatherer societies, males typically provide hunted meat while females gather fruit and vegetable foodstuffs (Hawkes 1993). Nevertheless studies indicate that male food production exceeds male food consumption (Kaplan et al 2000; Gangestad 2007), with males being found to provide an average of 66% of foods in hunter-gatherer societies (Kaplan et al 2000) and a similar proportion of calories in foraging societies (Gangestad 2007). This parental investment could have taken the form of direct provisioning of the hunter’s nuclear family or provisioning of the whole group, as outlined above (Hawkes et al 1985; Kaplan & Hill 1985; Hill & Kaplan 1988; Hawkes 1991; Hill & Hurtado 1996; Smith 2004). There is thus evidence for such an evolutionary response having occurred.

One strategy by hominid mothers to deal with a need for an increasing volume of parental investment may therefore have been for her to attract, choose and retain mates able to provision and protect her offspring and herself on a prolonged basis. In this environment displays of altruistic behaviour such as caring and generosity towards others and bravery on behalf of a group may well have acted as reliable and ‘honest’ cues for hominid females in selecting mates most willing to provision and protect her and her offspring in the longer term. If so, selection on female mate preference towards altruistic traits is likely to have been strong. The importance of this point was recognised by Buss (1989) in the context of female mate preference towards cues indicating resource provision in males:

> 'Future research is needed…to examine characteristics that signal not just the capacity to acquire resources, but the male's willingness to devote those resources to a female and her offspring.' (Buss 1989).

2.7.3 The Cost to Fitness of Mate Preference towards Altruistic Traits

Mate preference towards altruistic traits is likely to reduce the fitness of the individual expressing it as surely as altruism itself if the preferred altruistic mate subsequently expends energy and takes risks on behalf of unrelated individuals in activities of no benefit to the fitness of the mate expressing the preference and her/his offspring. It may, therefore, appear paradoxical that such a mate preference could have been favoured, even under the conditions suggested above.

Providing, however, that the phenotypic benefits of increased parental investment (Kirkpatrick & Ryan 1991) exceeded the costs of mate preference towards altruistic traits, then genes associated with such a preference could have increased in frequency. By the same token, providing that altruistic displays served as 'honest' cues to superior genetic and phenotypic quality under the 'handicap principle' (Zahavi 1977, 1995), then genes associated with a mate preference towards them could also have been favoured. Theoretical modelling of 'runaway' selection (Fisher

1958) has demonstrated that the genetic correlation between mate preference and preferred trait can result in a powerful selective process (e.g. Lande 1981). Thus mate preference towards altruistic traits may also have been favoured under the ‘runaway’ mechanism. The suggested scenario is also relevant to the evolution of human altruism under the sensory bias and genetic compatibility mechanisms.

2.7.4 How Other Human Characteristics might have Promoted Sexual Selection on Altruistic Traits

Miller’s memorable suggestion that with the evolution of language ‘thought itself became subject to sexual selection’ (Miller 2000, p. 10) carries with it an important point about the hypothesised link between sexual selection and human altruism. The evolution of language allied to more advanced intelligence and improved memory are likely to have made ‘sexual gossip’ (Miller & Todd 1998) a prominent feature of life in ancestral populations. This is particularly likely under the conditions recognised by anthropologists as being typical of hunter/gatherer societies – that is, where individuals live in relatively small groups but where there is mobility and interchange of individuals between groups (Chagnon 1979; Kaplan & Hill 1985; Hill 2002).

With ‘sexual gossip’ (Miller & Todd 1998) reported incidents of altruistic acts such as kindness or cooperation towards others and bravery in defence of a group could have been communicated on a widespread basis and over long timescales. Sophisticated evaluation of potential mates could have occurred and the quality of the reported altruistic behaviour could have been assessed with attempts at sham altruistic behaviour (i.e. showy displays that involve little sacrifice or risk) being identified. Thus human communication, allied with advanced intelligence and improved memory, could have strongly promoted the ‘honesty’ of signals related to altruistic behaviour.

A further important aspect of ‘sexual gossip’ (Miller & Todd 1998) is that displays of altruistic traits would not have needed to be confined to overtly mating contexts (i.e. altruistic acts directly involving potential mates). Instead, ‘sexual gossip’ would have involved reports of altruistic behaviour in all contexts - including those where altruistic and cooperative action on behalf of a group took place. As a result, sexual selection could have delivered a substantial reproductive premium to a successful altruist without the immediate stimulus of overt reproductive competition.

Concealed ovulation in females is also likely to have made mate guarding by males who relied on strength and intimidation alone as a mating strategy far more difficult. It is thereby likely to have increased scope for females to choose attractive mates (i.e. where mates display preferred behaviours such as altruism towards non-kin) and to subsequently be fertilised by them (Benshoof & Thornhill 1979; Miller 2000, p. 235). Year-round fertility is also likely to have contributed to this effect.

2.8 Plan for Thesis

In this thesis human altruism towards non-kin will be the subject for the following reasons:

- Humans are considered unusual in displaying altruism towards non-kin more prominently than other species (Fehr & Fischbacher 2003; Van Vugt et al 2007);
- Most of the empirical evidence for a link between sexual selection and altruism obtained so far relates to humans (e.g. Kelly & Dunbar 2001). This work thus provides a foundation upon which to build this thesis;
- It has been suggested that sexual selection may have acted powerfully on humans (Darwin 1871; Miller 2000) and there are grounds for envisaging conditions favourable to selection for human altruistic traits in human evolution (see Section 2.7).

In testing for a possible link between intersexual selection and human altruism towards non-kin the focus will be on measuring mate preference towards altruistic traits rather than the preferred trait – altruistic behaviour. The mate preference is seen as being far more indicative of the possible presence of sexual selection than concentrating on altruistic behaviour itself. Here, a major influence has been David Buss's work and particularly his cross-cultural study of mate preference (Buss 1989).

The first priority will therefore be to develop an accurate, reliable and valid measure of mate preference towards altruistic traits. In Chapter 3 the development of a psychometric scale, the mate preference towards altruistic traits (MPAT) scale, will be reported.

In Chapter 4 the MPAT scale will be employed to test whether mate choice on the basis of altruistic traits is actually occurring in a modern population – a necessary condition for sexual selection to take place. To this end, the scale will be administered to a sample of subjects who have already made a mate choice. Responses to the scale will then be correlated with those towards another psychometric scale designed to measure 'altruistic personality' (the Self-Report Altruism (SRA) scale (Rushton et al 1981)). Thus an assessment can be made of whether degree of mate preference in one spouse or partner correlates with the desired degree of preferred trait in the spouse or partner actually obtained. An inference can then be drawn as to whether human mate choice is influenced by altruistic traits in a modern population.

Chapter 5 will be concerned with sex differences in mate preference towards altruistic traits, as measured by the MPAT scale. The proposed scenario, discussed above, for how human altruism towards non-kin might have evolved suggests intense selection acting on this female mate preference. A stronger female response to the MPAT scale will therefore be predicted and tested here.

In Chapter 6 a necessary condition for sexual selection to take place - whether mate preference towards altruistic traits and 'altruistic personality' are subject to genetic influence - will be examined. Using a twin study design, correlations between the responses of identical and non-identical twins to the MPAT and SRA scales will be compared and an estimate of heritable variation in responses to the two scales will be made. If heritable variation can be found this would be consistent with sexual selection having acted on altruism towards non-kin. It is thought to be the first time that such a methodology has been employed to investigate the possible presence of sexual selection acting on a human trait.

In Chapter 7 the focus will move to altruistic behaviour itself through an examination of six motivations that prompt individuals to carry out voluntary work on behalf of others. Two psychometric measures – the SRA scale and the Volunteer Functions Inventory (VFI) – will be administered to a sample of volunteers. Conclusions will then be drawn as to the effect each of the six motivations has on volunteer commitment.

2.9 Summary

- Darwin's theory of sexual selection, although ignored or rejected for a hundred or so years after his death, has now become one of the fast-growing and important areas for research in modern biology.
- Extensive evidence of sexual selection has been found in many species.
- A body of theory exists to account for why one sex usually exercises mate choice and the other sex typically displays the preferred trait under intersexual selection. It is also capable of explaining mutual sexual selection.
- Various mechanisms, including the 'handicap principle', have been put forward to explain the basis upon which mate choice is made.
- Zahavi has proposed that altruistic behaviour towards non-kin evolved as a 'costly signal' of individual quality to others, including potential mates. Here, the fitness advantage of 'costly signalling' under sexual selection is seen as likely to be greater. Altruism may also have been favoured by sexual selection mechanisms other than the 'handicap principle'.
- Empirical evidence from studies of modern human populations suggests that traits analogous to altruism are valued in a potential mate. In particular, evidence of successful hunters in modern hunter/gatherer societies, acting in ways that can be interpreted as altruistic, are seen as consistent with a link between sexual selection and human altruism.
- A scenario in which conditions during human evolution that might have favoured the evolution of altruism towards non-kin is outlined.
- This thesis will use a psychometric scale developed to measure mate preference towards altruistic traits to test for sexual selection acting on these

traits. It will be employed in three different study designs. In a further study altruistic behaviour itself will be examined and conclusions drawn as to what motivations influence this behaviour.

CHAPTER 3. THE DEVELOPMENT OF THE MATE PREFERENCE TOWARDS ALTRUISTIC TRAITS (MPAT) SCALE (STUDY 1)

3.1 Introduction

3.1.1 Mate Preference as the Key to Testing for a Link between Altruistic Behaviour and Sexual Selection

The major problem that altruism represents for Darwinian biology was discussed in Chapter 1. It was concluded that current theory that seeks to explain altruism towards non-kin (e.g. Trivers 1971; Leimar & Hammerstein 2001; Wilson & Sober 1994; Brown1983; Lumsden & Wilson 1981; Blackmore 1999) has difficulty in fully resolving this problem. In Chapter 2 an alternative account of how altruism evolved was outlined, based on sexual selection. Darwin (1871) envisaged sexual selection taking two forms. The first, since termed intrasexual selection, involves contests or intimidatory displays, usually between males, with the females remaining passive throughout. The second, since called intersexual selection, involves displays of preferred traits, typically by males, with the females choosing mates on the basis of these displays.

Zahavi (1977, 1995, 2003; Zahavi & Zahavi 1997) was the first to propose a connection between intersexual selection and altruism towards non-relatives. He suggested that displays of altruistic behaviour were handicaps under his 'handicap principle' which, if successfully overcome, gave an 'honest' signal of superior genetic quality to others, including potential mates. In this thesis, the focus is on 'signalling' to potential mates through altruistic behaviour by means of sexual selection as it is seen as likely to confer a greater fitness advantage. The 'handicap principle' is regarded as a form of indicator mechanism under sexual selection (Andersson 1994; Andersson & Simmons 2006) but a number of other mechanisms have also been proposed to account for how sexual selection works (Andersson 1994; Andersson & Simmons 2006). As discussed in Chapter 2, these could have equally favoured the evolution of altruistic traits. These mechanisms work through an interaction between a mate preference expressed in one sex and a preferred trait expressed in the other. In examining the sexual selection hypothesis it was decided to concentrate on measuring mate preference towards altruistic traits because:

- Mate preferences have been studied widely in other studies that have investigated a link between sexual selection and human traits (e.g. Buss 1989) and so provide a foundation of research with which to make comparison;
- Mate preference is an essential element of intersexual selection (Andersson & Simmons 2006) and thus provides a key test of its presence. In contrast, the preferred trait, altruistic behaviour, is open to explanation by other theory and is thus less specifically indicative of a sexually selected origin.

A first requirement was therefore to locate a psychometric scale capable of measuring mate preference towards altruistic traits. No suitable scale could be found in the literature and so an initial objective was to develop such a measure. The development of this psychometric scale will form the subject matter of this chapter.

3.1.2 Issues Involved in Measuring Mate Preference towards Altruistic Traits

A number of issues were identified early on in the development of this psychometric scale. Firstly, altruistic traits are often culturally prescribed in human societies and so this issue had to borne in mind from the very beginning. The scale must therefore reflect the context of the society in which it is to be used. This point is no more clearly reflected than in the issue of gender. Cultural factors particularly influence the roles that females and males typically perform when carrying out altruistic acts (Eagly & Crowley 1986). The wording of items in a scale used to measure mate preference towards altruism could very easily suggest the sex of the altruist and thereby introduce bias in the way subjects of different sex express mate preference towards them (Zohar & Guttman 1989). Every effort was therefore made to include items in the psychometric scale that were as gender neutral as possible.

Another issue that was confronted early on was whether the altruistic act described should involve a monetary reward. Many altruistic acts performed in modern societies involve a monetary reward (e.g. a professional fireman rescuing a child from a burning house). The individual concerned is, in one sense, meeting the definition of altruism put forward in Chapter 1 but it could be argued that s/he is paid to perform altruistic acts on occasion and is not, on balance, incurring a net cost to fitness. There is a contrary argument here – that in choosing a career where altruistic behaviour is involved an individual may still be viewed as acting altruistically. Such examples have been used in another study of altruistic behaviour (Kelly & Dunbar 2001). Also, in certain situations, a rewarded individual may be able to choose whether to take or avoid a serious risk, thus demonstrating altruistic behaviour or the opposite. However, on balance, it was decided to avoid this possibly confounding issue by excluding items that imply monetary gain from the psychometric scale.

According to the classic model of error measurement the final set of items in a psychometric scale should be derived randomly from all possible items relevant to the trait being measured (Kline 1986, 2000). Under this model the ‘true score’ is the score that a subject would theoretically obtain if s/he could be given all those possible items to respond to. Thus the error of a test is affected by the extent to which the sample chosen reflects all these potential items (Kline 1986). To be representative, all items must also be relevant to the environment in which subjects would ordinarily make judgements about the desirability of a particular mate.

3.1.3 Definitions of Terms Used in Developing and Testing the MPAT Scale

Any psychometric measure must be able to demonstrate reliability and validity (Oppenheim 1992; Loewenthal 1996; Kline 1998). Reliability is concerned with a scale’s consistency and is a measure of the strength of association or homogeneity between the items of the scale (Kline 1986, p.12; Loewenthal 1996, p.5). Reliability can be assessed by a number of methods including:

- **Internal consistency**. This is the correlation between scores in response to each individual item with the total score of the scale. In other words, it is a measure of how well each item relates to all the other items in the scale (Loewenthal 1996). Cronbach’s coefficient alpha (α) is usually seen as its most desirable measure (Loewenthal 1996). A coefficient of at least 0.70 can be seen as a minimum standard (Loewenthal 1996, p.10), although others claim 0.80 as the required minimum (Oppenheim 1992, p. 283; Loewenthal 1996, p.48);

- **Test/retest reliability**. This is the correlation in score totals of the same subjects responding to the same scale twice over a period of time (Loewenthal 1996, p. 9; Kline 1998, p.29). It is thus a measure of the temporal stability of responses to the scale. The period that lapses between test and retest must be sufficient for subjects not to be able to remember how they responded on the first occasion.

In contrast, the validity of a psychometric scale is concerned with whether the scale actually measures what it is claimed to measure (Oppenheim 1992, p. 144; Loewenthal 1996, p.12). There are various types of validity of which the most simple is face validity – that is, whether the scale looks as if it manifestly measures what it is claimed to measure (Kline 1998). However, in the field of attitude and personality testing face validity is generally not seen as an adequate guide of validity (Kline 1998, p.35). A range of more rigorous methods of measuring validity is available:

- **Construct validity.** This is a measure of the extent to which responses to the new scale correlate with those towards a similar construct or concept that is measured by an already established scale (Oppenheim 1992, p. 162; Loewenthal 1996, p.55; Kline 1998, p.35);
- **Predictive validity.** This is a measure of how well a scale predicts a relevant criterion (Oppenheim 1992, p. 162; Kline 1998, p. 35);

3.1.4 Objective of this Study

The objective of this study is therefore to develop a new psychometric scale, henceforward referred to as the Mate Preference Towards Altruistic Traits or MPAT scale. Its internal consistency and test/retest reliability will be tested using the sample employed in this study along with an initial test of its construct validity. The testing of a new scale, however, is an ongoing process and further tests of its reliability and initial tests of its validity will be reported in later chapters.

3.2 Methods

3.2.1 Development of Item Pool

Bearing in mind the definition of altruistic behaviour given in Chapter 1 (i.e. ‘any act that has the effect of increasing the reproductive success of another organism at the expense of that of the altruist’), and the criteria discussed above, an initial set of items was prepared containing hypothetical examples of reported altruistic behaviour in a potential mate. A volunteer focus group comprising five final year undergraduates and two postgraduate students from the School of Biology at the University of Nottingham was assembled to assess the item pool produced. The focus group met on Tuesday 27 November 2003 and subjects were asked whether:

- each item was clear and unambiguous;
- if not, whether they could suggest an alternative wording;
- they could suggest further suitable items;

- they thought financial gain was implied in any of the items and, if so, how the wording could be changed to avoid this impression;
- any items implied someone of a particular gender.

As a result, changes were made to the wording of existing items, some items were removed and new items introduced. A revised set of items was then presented to a further 14 subjects who were either members of staff or postgraduate students in the School of Biology, University of Nottingham. The various items were reviewed in open-ended discussion in the light of the issues discussed in the focus group and further amendments to the items were made.

Finally, a pool of 51 items was identified, representative of altruistic traits in a potential mate. The optimum ratio between size of item pool and number of items comprising the final scale has been suggested as being about one to two (Loewenthal 1996, p.22) or one to four or five (Oppenheim 1992, p. 174). On the basis of the latter more conservative rule of thumb this item pool appeared sufficiently large to generate a scale of at least ten items. Some items were positive (e.g. ‘Is generous towards other people’) and others negative (e.g. ‘Not bothered about being thought stingy towards other people’) so as to encourage subjects to think carefully about each response rather than falling into a pattern of routinely ticking the same column (Oppenheim 1992).

3.2.2 The Questionnaire

The next stage was to administer the item pool to a sufficiently large sample of subjects to obtain data that could then be used to derive a sound psychometric scale. A questionnaire was therefore designed with the 51 items were arranged at random and presented in the form of a Likert-type scale in which subjects were asked to rate each item under one of five categories - 'Very Undesirable', 'Quite Undesirable', 'Neither Desirable nor Undesirable', 'Quite Desirable' and 'Very Desirable' (see Appendix 3.1). The instructions given were as follows:

'Rate the following statements according to what you think is desirable or undesirable in someone with whom you would like to have a relationship (a future husband, wife, boyfriend, girlfriend). Please take your time and think carefully before placing a tick in one of the boxes.'

Ratings by subjects of each item in response to the five-category Likert-type scale were scored from 0 to 4 to reflect low through to high desirability. A page requesting certain demographic details such as age, sex, religion and ethnic classification was added (see Appendix 3.2) along with a consent form which subjects were asked to complete and sign to acknowledge their agreement to take part in the study (see Appendix 3.3). The consent form was then separated from the rest of the questionnaire prior to data inputting to preserve the confidentiality of each subject's responses.

A psychometric scale (Hill 1945) developed to measure preference towards some 18 characteristics in potential mates (e.g. 'dependable character', 'sociability'), was also included in the questionnaire. The scale had been widely used, most notably, in a major cross-cultural study of mate preferences (n = 10,047) across 37 cultures (Buss 1989; Buss et al. 1990). This scale will henceforward be referred to as the General Mate Preference (GMP) scale here for convenience of expression. One purpose of including it was to compare how subjects in this sample rated mate preference towards the 18 characteristics compared with subjects in the much larger cross-cultural study. As a result, an inference could be drawn as to how representative subjects in this sample were in terms of the way they generally rated mate preferences – and therefore how representative they might be in terms of the specific example of mate preference towards altruistic traits.

Subjects were asked to rate the 18 characteristics of the GMP scale on a similar basis to that used in Buss's (1989) study. That is, a four-point scale was used ranging from 'Very Unimportant', 'Quite Unimportant', 'Quite Important', to 'Very Important' and scored from 0 to 3 (see Appendix 3.4).

3.2.3 Arrangements for Testing of Item Pool

Permission was obtained to carry out surveys in four halls of residence at the University of Nottingham and these took place during April and May 2004. I was present on one day outside the dining area of each hall of residence prior to and during the lunch and supper times. This gave me an opportunity to ask students to complete the questionnaires while they were waiting. They also completed the questionnaires while eating their meals or to took them away and returned them later that day. I approached students individually or in groups, asking whether they would be interested in completing a questionnaire on their mate preferences and personality characteristics. No more specific information about the purpose of the study was given at that stage, although I said that I was willing to give more information after they had completed the questionnaire. Only a few took advantage of this offer, which was undertaken out of the hearing of those still completing the questionnaire. I emphasised that the process was confidential and that the consent form would be separated from the questionnaire immediately afterwards. The overall response was enthusiastic and inquisitive and only very occasionally was a request to complete the questionnaire refused.

3.2.4 Screening of Items

The data were then analysed using SPSS version 14.0. To eliminate items that discriminated poorly between the responses of subjects and to facilitate later principal components analysis the skewnesss and kurtosis of each item was measured. The tendency for items to elicit responses that cluster towards one end of the spectrum of response is measured by skewness while kurtosis is the relative degree of sharpness of the peak in the distribution curve of responses (Anastasi 1988; Ferguson & Cox 1993). Excess skewness was determined by dividing the skewness parameter value of each item ($g1$) by its standard error and where the resulting value exceeded 2.00 the item was removed (E. Fergusson; personal communication). Where the value for the kurtosis parameter ($g2$) was greater than 2.00 that item was also removed (E. Fergusson; personal communication).

The remaining items were then subject to principal components analysis, which is an essential tool in scale construction (Kline 1994). It measures correlations between all items (Kline 1994) and then extracts orthogonal variables that express variation in the original inter-correlated variables. The aim was to identify items that grouped together under a single general component (Kline 1994). The size of the sample needed for successful principal components analysis is dependent on the number of items being analysed. A ratio between subjects and items of 2:1 is seen as a minimum with a higher ratio being preferable (Kline 1994, p. 74). As the responses of both sexes were of interest a minimum sample size was therefore 51 items x 2 x 2 = 204 subjects.

3.2.5 Testing of Final Version of MPAT Scale

The final version of the MPAT Scale will be tested in this study and in four other studies, providing a comprehensive test of its reliability and validity. In this study the MPAT scale will be tested in a sample of undergraduate students at the University of Nottingham (*n* = 380; mean age = 19.4 years) while its test/retest reliability will be examined in another sample of undergraduate and graduate students at that University (*n* = 52).

The reliability of the MPAT scale will be measured by assessing its internal consistency using Cronbach's coefficient alpha (α). Test/retest reliability was measured here by including items from the MPAT scale at random with those from the GMP scale and additional items discarded from the original item pool. The object of including these other items was to reduce the possibility of subjects being able to remember their responses to the MPAT scale. To preserve the confidentiality of the process subjects were asked to enter their student 'smartcard' numbers so that a link could be made between the test and retest responses without subjects having to give their names. A copy of the questionnaire employed can be found in Appendix 3.5. The test/retest reliability exercise was carried out during April and May 2005 with a period of 14-21 days elapsing between the initial test and the repeat of the exercise. An initial test of the construct validity of the MPAT scale was carried out in this study by correlating responses to it with those towards the GMP scale, which assesses the construct of mate preference.

3.3 Results

3.3.1 Characteristics of the Sample

A detailed demographic breakdown of the sample obtained can be found in Table 3.1. The key points were that 380 subjects responded to the questionnaire (185 females and 190 males), with a mean age of 19.4 years. This well exceeded the estimated minimum sample size of 204 deemed necessary to carry out adequate principle components analysis, as discussed above. The sample proved homogeneous in relation to most of the demographic categories to which subjects were asked to respond, with subjects being mostly single, heterosexual, British and White European.

Table 3.1. Demographic breakdown of subjects in Study 1

Category		**Response**
Gender	Female	185
	Male	190
	Undisclosed	5
Mean Age	Years (± s.e.)	19.4 (0.07)
Marital Status	Single	378
	Married	0
	Undisclosed	2
Are you currently in a close relationship?	Yes	145
	No	230
	Undisclosed	5
Would you describe yourself as heterosexual?	Yes	366
	No	14
	Undisclosed	15
Are you a UK national?	Yes	326
	No	53
	Undisclosed	1
Ethnic Group	White European	326
	African	6
	Afro-Caribbean	1
	Indian	18
	Other Asian	16
	Other	9
	Undisclosed	4
Religion	Anglican	77
	Catholic	44
	Other Christian	66
	Agnostic/Atheist	128
	Buddhist	4
	Hindu	10
	Islam	3
	Sikh	3
	Other	36
	Undisclosed	9

A test was then carried out to measure how typical this sample was in terms of how it assessed mate preferences in general. How subjects in this sample rated items in the GMP scale (Hill 1945) was compared with how subjects in the cross-cultural sample collected by Buss et al (1990) rated them. In both the female and male samples very strong positive correlations between this study and the cross-cultural study were found (Spearman Rank Correlation: $r_s = 0.96$, $p = < 0.001$ and $r_s = 0.91$, $p = < 0.001$ respectively; $n = 18$) (see Table 3.2).

Table 3.2. Correlation between ranking of responses to the General Mate Preference (GMP) Scale in the present sample and those in the cross-cultural sample (Buss 1989). Female Sample:

Variable	Sample in Study 1		Cross-Cultural Sample (Buss 1989)	
	Rank	Mean Rating	Rank	Mean Rating
Mutual attraction-love	1	2.887	1	2.87
Dependable character	2	2.659	2	2.69
Emotional stability and maturity	3	2.532	3	2.68
Education and intelligence	4	2.408	5	2.45
Sociability	5	2.309	6	2.30
Ambition and industrious	6	2.146	9	2.15
Pleasing disposition	7	2.128	4	2.52
Desire for home and children	8	2.125	8	2.21
Good health	9	1.946	7	2.28
Similar education	10	1.940	11	1.84
Good looks	11	1.865	13	1.46
Good financial prospect	12	1.717	12	1.76
Refinement, neatness	13	1.415	10	1.98
Similar religious background	14	1.238	16	1.21
Favourable social status or rating	15	1.277	14	1.46
Good cook and housekeeper	16	1.151	15	1.28
Similar political background	17	0.822	17	1.03
Chastity	18	0.674	18	0.75

Male Sample:

Variable	Sample in Study 1		Cross-Cultural Sample	
	Ranking	Mean Score	Ranking	Mean Score
Mutual attraction-love	1	2.773	1	2.81
Dependable character	2	2.370	2	2.50
Emotional stability and maturity	3	2.279	3	2.47
Sociability	4	2.223	7	2.15
Good looks	5	2.206	10	1.91
Education and intelligence	6	2.196	6	2.27
Good health	7	2.069	5	2.31
Pleasing disposition	8	2.066	4	2.44
Ambition and industrious	9	1.808	11	1.85
Desire for home and children	10	1.725	8	2.09
Similar education	11	1.614	14	1.50
Refinement, neatness	12	1.547	9	2.03
Good cook and housekeeper	13	1.258	12	1.80
Favourable social status or rating	14	1.185	15	1.16
Good financial prospect	15	1.154	13	1.51
Similar religious background	16	1.122	17	0.98
Similar political background	17	0.853	18	0.92
Chastity	18	0.762	16	1.06

A further test of how representative this sample was lay in whether it replicated the results found by Buss (1989) in relation to the target variables he tested in his study. The significantly greater female mate preference found by Buss (1989) in response to ‘Has good financial prospects’ and ‘Is ambitious and industrious’ was replicated here (independent samples t-test: $t_{370} = 7.14$; $p < 0.001$ and $t_{370} = 4.79$; $p < 0.001$ respectively). Similarly, a significantly greater male mate preference was found towards ‘Is good looking’ ($t_{372} = 5.37$; $p < 0.001$), also replicating Buss’s finding. Only in the case of mate preference towards chastity ‘Has no prior sexual experience’ was a non-significant result found ($t_{371} = 1.04$; $p = 0.300$) in contrast with 23 out of 37 societies in Buss’s study where a significant result was demonstrated in the direction of greater male preference. However, when the results of the British sample obtained by Buss ($n = 130$) were examined they were found to conform with the results found in this sample in relation to all four variables.

3.*3.2 Item Screening*

The 51 items screened are detailed in Table 3.3. Of these, 34 items exceeded the maximum desirable level of skew ($g1/SE_{g1} > 2.0$) and/or had values for kurtosis that exceeded 2.0 ($g2 > 2.0$). These items were therefore removed. A total of 17 items remained. One item, ‘Is a member of a Lifeboat Crew’ was, on further reflection, considered to be insufficiently gender-neutral and so was removed at this stage.

Table 3.3: Item pool used in development of Mate Preference Towards Altruistic Traits (MPAT) Scale

Item	Skewness/ S.E of skewness ($g1/SE_{g1} > 2.0$)	Kurt-osis ($g2 > 2.0$)	Other comments
Is generous towards other people	4.93	1.73	
Is willing to stand by friends 'through thick and thin'	7.84	0.678	
Spent a year helping children in an African orphanage	2.02	1.80	
Not bothered about being thought stingy towards other people	1.83	0.12	Removed due to loading of only 0.142 on component 1
Once defused a violent argument between two friends	1.86	1.06	Removed due to Communality of 0.167
Occasionally willing to be dishonest if it pays	1.74	0.54	Removed due to loading of only 0.173 on component 1
Cares about the welfare of animals	3.52	0.50	
Preferred not to become involved when a friend was in danger	8.90	2.45	
Ran the London Marathon to raise money for a good cause	1.22	0.76	Included in MPAT Scale
Is always willing to give money to charity	2.36	0.52	
Once dived into a river to save someone from drowning	1.03	0.22	Included in MPAT Scale
Refused to help a friend in need	9.24	1.40	
Took part in a sponsored parachute jump to raise money for a charity	2.85	0.07	
Usually leaves a large tip in an expensive restaurant	0.60	1.46	Removed due to loading of only 0.215 on component 1
Is a 'giver' rather than a 'taker'	7.12	2.22	
Got our of helping at a children's Christmas party	0.99	0.21	Removed due to a Communality of 0.167
Regularly helps an elderly neighbour	1.45	0.55	Included in MPAT Scale
Donates blood regularly	0.06	0.83	Included in MPAT Scale
Not particularly bothered about other people	10.78	1.57	
Willing to 'do the right thing' even if it is risky to do so	4.87	0.78	
Tipped off the police about a local drugs dealer	2.17	0.29	
Volunteered to help out in a local hospital	0.67	0.41	Included in MPAT Scale
No longer acknowledges a friend who 'has gone down in the world' socially	10.28	1.53	
Has a caring attitude towards other people	3.87	0.72	
Usually tries to get out of paying for a round of drinks	5.63	0.29	
Is willing to rescue someone in danger	6.53	3.18	
Always willing to help other people's children	3.55	0.90	
Had information about a terrorist	4.17	0.20	

attack but kept quiet for fear of retaliation			
Once cared for a stray dog injured by a car	1.17	0.57	Included in MPAT Scale
Is a member of a Lifeboat Crew	1.44	1.46	Removed on grounds of it not being gender neutral
Helped clear people away from a suspect package found in an airport	1.42	0.70	Included in MPAT Scale
Ended a friendship with someone wrongly accused of a serious crime	5.70	0.34	
Unwilling to take a risk to help people in an emergency	6.56	0.97	
Once spent a weekend helping repair a community hall without pay	2.97	0.96	
Thinks we'd all be better of if everybody looked after themselves	3.81	0.12	
Once intervened to protect someone being robbed by a youth	3.29	0.78	
Did not mind being thought a coward by refusing to help other people	2.94	0.30	
Got out of visiting a friend in a hospice	4.22	0.22	
Climbed a tree to rescue a neighbour's cat	0.17	1.01	Included in MPAT Scale
Volunteered to help without pay on a week's holiday for disabled people	1.04	0.03	Included in MPAT Scale
Once got someone out of a crashed car before it burst into flames	2.59	0.17	
Tends to be selfish towards other people	7.14	0.55	
Once refused to give money to help starving people in Ethiopia	2.02	0.14	
Took some rubbish abandoned in the street to a local tip	2.49	1.18	
Once gave a quarter of annual income to help a friend in dire financial trouble	4.20	0.12	
Brave if called upon to rescue others	4.44	1.27	
Had a pet put down rather than pay the vet's bill for an operation	1.79	0.67	Removed due to a Communality of 0.097
Once picked up a wallet dropped in the street and handed it into the police	4.08	0.98	
Is a member of a mountain rescue team	2.10	1.29	
Once stood by and let someone else rescue children trapped in a burning house	1. 51	0.03	Removed due to loading of only 0.222 on component 1
Gives time freely to help others out	7.47	2.35	

3.3.3 Principal Components Analysis

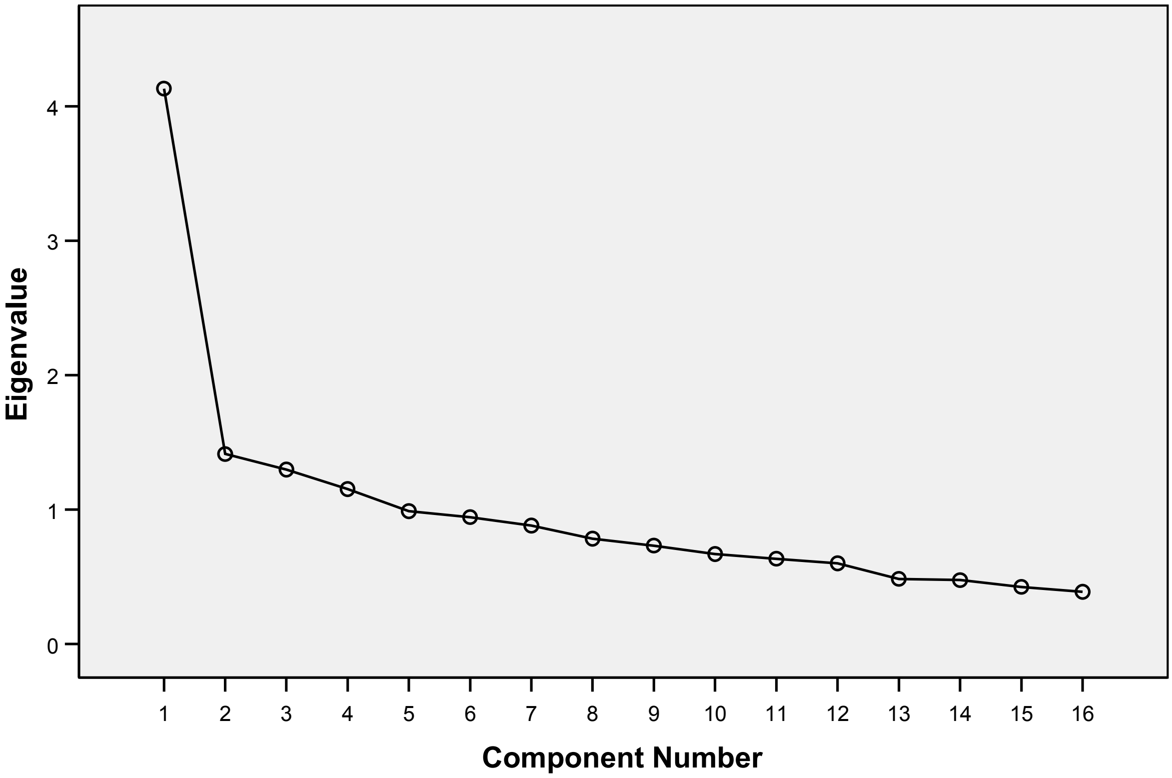
The 16 remaining items were then subjected to principal components analysis. Without specifying any number of components, items loaded onto four components as illustrated in Table 3.4:

Table 3.4. Component matrix from principle components analysis: loadings of 16 items

Items	Component			
	1	2	3	4
Volunteered to help without pay on a week's holiday for disabled people	0.710			
Volunteered to help out in a local hospital	0.702			
Regularly helps an elderly neighbour	0.658			
Once dived into a river to save someone form drowning	0.641			
Ran the London Marathon to raise money for a good cause	0.631			
Once cared for a stray dog injured by a car	0.605			
Climbed a tree to rescue a neighbour's cat	0.596			
Donates blood regularly	0.583			
Helped clear people away form a suspect package found in an airport	0.540			
Once defused a violent argument between two friends	0.408			
Got out of helping at a children's Christmas party	0.346			
Not bothered about being thought stingy towards other people		0.573		
Once stood by and let someone else rescue children trapped in a burning house		0.529		
Had a pet put down rather than pay the vet's bill for an operation		0.502		
Usually leaves a large tip in an expensive restaurant			0.608	
Occasionally willing to be dishonest if it pays				0.548

Scree plots are usually seen as offering the best solution to identifying the most appropriate number of components that should be retained after principle components analysis (Kline 1994, p.75). In this case, examination of the scree plot clearly indicated that a one–component solution was most appropriate (see Figure 3.1). This judgment was supported by 11 of the items loading onto component 1 above.

Figure 3.1. Scree plot from principle components analysis of 16 items



A one-component structure was therefore specified (see Table 3.5). In line with the convention that loadings must be above 0.3 to be considered salient (Kline 1994, p.53; Kline 1998, p.57) four items with loadings less than 0.3 were removed and the analysis run again.

Table 3.5. Component matrix from principle components analysis: loadings of 16 items with one component specified (items removed due to small loadings indicated with an asterisk)

Items	Loadings
Volunteered to help without pay on a week's holiday for disabled people	0.710
Volunteered to help out in a local hospital	0.702
Regularly helps an elderly neighbour	0.658
Once dived into a river to save someone form drowning	0.641
Ran the London Marathon to raise money for a good cause	0.631
Once cared for a stray dog injured by a car	0.605
Climbed a tree to rescue a neighbour's cat	0.596
Donates blood regularly	0.583
Helped clear people away form a suspect package found in an airport	0.540
Once defused a violent argument between two friends	0.408
Got out of helping at a children's Christmas party	0.346
Not bothered about being thought stingy towards other people	0.328
Once stood by and let someone else rescue children trapped in a burning house	0.222 *
Had a pet put down rather than pay the vet's bill for an operation	0.215 *
Usually leaves a large tip in an expensive restaurant	0.173 *
Occasionally willing to be dishonest if it pays	0.142 *

Three of the remaining 12 items were then found to have communalities well below 0.30, while one item was considered borderline (0.294). Communalities indicate the proportion of variance in each item for which that the component accounts and communalities around or below 0.30 are considered poor (Kline 1998, p.58). The three items whose communalities fell substantially below the 0.30 level were therefore removed while the borderline item was retained.

The program was run again and the component matrix for the resulting nine-item scale with the loadings for each item can be found in Table 3.6. The total variance explained was 41.219 %. The Kaiser-Meyer-Okin Measure of Sampling Adequacy was found to be 0.87, which is seen as good (Field 2005), while the Bartlett's Test of Sphericity was found to be significant ($p < 0.001$).

Table 3.6 Component matrix of items from principal components analysis comprising the Mate Preference Towards Altruistic Traits (MPAT) Scale (n = 373)

Items	**Loadings**
Volunteered to help out in a local hospital	0.739
Volunteered to help without pay on a week's holiday for disabled people	0.720
Regularly helps an elderly neighbour	0.682
Ran the London Marathon to raise money for a good cause	0.642
Once dived into a river to save someone from drowning	0.632
Donates blood regularly	0.613
Climbed a tree to rescue a neighbour's cat	0.591
Once cared for a stray dog injured by a car	0.591
Helped clear people away from a suspect package found in an airport	0.543

3.3.4 Were the Items Open to Other Criticism?

The resulting nine items were assessed with a view to identifying any that might be virtual paraphrases of each other - so-called ‘bloated specifics’ (Kline 1994, 1998, p. 160). Such items will, in practice, reduce the number of items in a scale that are capable of discriminating between the responses of subjects. I took the view that none fell into this category. Some items described personal risk, some involved a caring role, some suggested a sacrifice of personal time and energy and some demanded physical prowess. The range of those benefiting from the altruistic acts included the elderly, people with disabilities, the sick, other species, as well as the general public. Although some items might, arguably, be viewed as hinting at a more female ‘caring’ role or a more male ‘heroic’ role the overall balance across all nine items was seen as broadly gender-neutral. In sum, they were seen as representing a broad spectrum of altruistic behaviour towards non-kin in the society in which the scale was to be used.

3.3.5 Reliability and Validity of MPAT Scale

The internal consistency of the MPAT scale in this study, as measured by Cronbach’s coefficient alpha, was $\alpha = 0.82$ while its test/retest reliability was found to be $r_{50} = 0.76$, $p < 0.001$. The internal consistency of the GMP scale was found to be $\alpha = 0.72$. With regard to the construct validity of the MPAT scale, correlation with responses to the GMP scale was found to narrowly escape significance ($r_{343} = 0.11$, $p = 0.052$).

3.4 Discussion

A thorough and systematic process was followed to develop and test the MPAT scale. An item pool that described examples of altruistic behaviour in a potential mate was drawn up using a focus group and interviews with staff and postgraduate students. A sample of university students that well exceeded the minimum size needed to carry out principle components analysis then rated the relative desirability of altruistic items in a potential mate. Responses within this sample to the GMP scale were found to be very similar to those of a much larger cross-cultural study (Buss et al 1990), indicating that this sample was quite typical in terms of how it rated mate preference. Following item screening and principal components analysis nine suitable items were identified and incorporated into the MPAT scale.

The internal consistency of the MPAT scale in this study exceeded $\alpha = 0.80$, the minimum coefficient thought necessary (Oppenheim 1992, p. 283; Loewenthal 1996, p.48). This was achieved despite the MPAT scale containing fewer than ten items, a situation in which lower reliability coefficients can be expected (Loewenthal 1996, p. 48). The MPAT scale thus demonstrated strong internal consistency. Evidence of its test/retest reliability showed that it had satisfactory temporal stability.

The initial test of construct validity narrowly escaped significance. It must, however, be remembered that this study was primarily concerned with scale development. The final nine items were not administered to subjects in the form for which the MPAT scale was designed (i.e. ensuring that subjects would be blind to the prediction being tested). As all items concerned altruistic traits this was by no means certain. Thus construct validity needs to be tested using the final version of the MPAT scale. Testing the reliability and validity of a new scale is an ongoing process and so I will report on these points where the MPAT scale is employed in later chapters.

I concluded that I had a sound psychometric scale with which to start measuring mate preference towards altruistic traits. On this basis, I then felt able to proceed with testing the three predictions contained in this thesis and exploring other patterns revealed by the MPAT scale.

3.5 Summary

- A pool of items describing examples of altruistic behaviour in a potential mate was derived and administered to a sample of 380 subjects.
- Items with responses that demonstrated unacceptable levels of skewness and kurtosis were removed and the remaining items subjected to principal components analysis.
- A single general component was identified and after removal of further items the final version of the mate preference towards altruistic traits (MPAT) scale was obtained.
- The internal consistency of the MPAT scale was tested and found to exceed the minimum standard required. The new scale’s test/retest reliability was also found to be satisfactory.
- The reliability and validity of the MPAT scale will be tested in later studies.

CHAPTER 4. HUMAN MATE CHOICE AND ALTRUISM TOWARDS NON-KIN (STUDY 2)

4.1 Introduction

4.1.1 Mate Choice as Evidence for Sexual Selection

Sexual selection arises from differences in reproductive success caused by reproductive competition (Andersson 1994). These differences in reproductive success are associated with particular sexually selected characters such as antlers, horns, bright colouring, increased aggression, size dimorphism and courtship displays which are favoured during reproductive competition. Many studies of intersexual selection have investigated whether mate choice acts to favour certain preferred traits and have been able to demonstrate the process at work in numerous species and in both sexes (Andersson 1994, p. 127-142). Intersexual selection mechanisms are seen as operating through genes linked to a mate preference expressed in one sex and genes linked to a preferred trait expressed in the other (Andersson & Simmons 2006).

If sexual selection were currently acting on human altruistic traits we would expect to see mate choice on the basis of altruistic traits taking place in modern human populations. In Chapter 3 a psychometric scale designed to measure mate preference towards altruistic traits was developed (the MPAT scale). We would therefore expect the mate preference (as measured by responses to the MPAT scale) to correlate significantly with responses to a psychometric scale that measures the preferred trait (in this case, the altruistic behaviour typically displayed) in the mate chosen. In this chapter I therefore look for such a correlation by examining the responses of a sample of subjects who have made a choice of a long-term mate – that is, husbands, wives or partners in long-term relationships.

Human mate choice is constrained by a host of factors including local availability of suitable mates, parental preferences, sex ratio and the nature of the mating system (Buss 1989). Mate choice on the basis of altruistic traits is thus one factor among many others that may influence mate choice and therefore any statistical relationship between mate preference and preferred trait is unlikely to be strong. Furthermore, a wide range of variables may bias or confound mate choice acting on altruistic traits but every effort will be made to take account of these in the study. These variables include a tendency by subjects to give a socially desirable rather than a true and accurate response, the tendency for 'like to prefer like' in mates and length of time that couples have lived together influencing the degree to which their responses conform. The following was therefore tested:

Prediction 1: Mate preference towards altruistic traits in one spouse/partner, as measured by the MPAT scale, will correlate significantly with a measure of the preferred trait (i.e. altruistic behaviour typically displayed in the spouse/partner chosen).

4.2 Methods

4.2.1 The Sample

The Twin Research and Genetic Epidemiology Unit, based at Hospital, London, UK, was approached in connection with a study that will be reported in Chapter 6. The agreement of the Director was obtained to allow access to twins on their registry and for data collection for this study as well. The unit regularly organised 'twin days' in which a sample of 50 or so twin pairs attended one location and took part in a range of scientific tests and studies. I attended six 'twin days' held between August 2005 and April 2006, all but one of which took place at St. Thomas's Hospital, London. The other location was at the University of Leeds. Those twins who reported that they were married or living in long-term relationships were requested to respond to a questionnaire and take a copy of it home with a view to asking their spouses/partners to complete it. Subjects were urged verbally and in writing not to influence the responses of their spouses/partners when these subsequently completed the questionnaire. They were told that they were taking part in a study of mate preferences and other human characteristics and no mention was made of altruistic traits.

4.2.2 The Measure of Altruistic Behaviour

A search of the literature identified a suitable psychometric scale to measure altruistic behaviour - the Self-Report Altruism (SRA) scale (Rushton et al. 1981). The SRA scale requests subjects to rate the frequency with which they have carried out some 20 different altruistic acts in the past using five categories - 'Never', 'Once', 'More than Once', 'Often' and 'Very Often'. Individual items were scored from 1 to 5 with the total score thus ranging from 20 to 100.

The internal consistency of the SRA scale has been found to be good (Rushton et al 1981) while its validity has been demonstrated by a significant correlation being found with ratings by peers of the degree of the subject's altruistic behaviour (Rushton et al 1981). Validity has also been confirmed by correlating responses to the scale with those towards other measures of altruism (Rushton et al 1981).

A later study (Rushton et al 1986) assessed the heritability of responses to the SRA scale by employing a twin study design. It was estimated that 56% of the variation in responses could be explained by broad sense heritability, a finding that led Rushton et al (1981, 1986) to conclude that altruistic traits are expressed consistently over time and can be used to define 'altruistic personality'.

4.2.3 Social Desirability in Responses

In most human societies altruism is an aspect of behaviour that is likely to be heavily influenced by social norms and cultural influences. There is therefore a danger that data obtained in response to the MPAT and SRA scales might be a reflection of socially desirable responses or culturally acceptable norms rather than being an accurate reflection of the subject's behaviour. Faced with responding to a scientific questionnaire in a setting that they might well find slightly intimidating, subjects could well feel prompted to give the responses that they think are expected of them or be tempted to exaggerate their responses in line with what they perceive as desirable by others or themselves.

Fortunately, this problem has long been recognised by practitioners in the field (e.g. Crowne & Marlowe 1964) and can be measured and controlled for using a social desirability (SD) scale. In the scale chosen for this study (Crowne & Marlowe 1964) subjects were presented with a list of 33 culturally acceptable but probably untrue statements (e.g. 'I am always courteous, even to people who are disagreeable', 'I'm always willing to admit it when I make a mistake') in a true/false format. The extent to which subjects favoured what they saw as socially desirable, but probably incorrect, statements was measured. If scores in response to the SD scale correlate with those in response to the psychometric scale measuring the trait of interest then one can reasonably infer that a similar degree of exaggeration was also present in responses to that scale. Social desirability can therefore be taken account of in statistical analysis of responses.

4.2.4 Length of Relationship

A study design that sets out to measure whether mate choice is occurring on the basis of particular traits should, ideally, take place at the actual point when the mate choice was made – and not many years later as is likely to be the case here. It could be argued that, as couples are likely to grow more alike as a result of living together in close proximity for much of their lives, any correlation between spouses/partners could be explained as an effect of the length of their relationship and not what had motivated their original mate choice. In fact, what research there is on this question suggests, paradoxically, that couples married longer are less alike than those married recently (Buss 1985). However, to deal with this objection subjects were asked to report the length of their relationship. This variable can therefore be used in statistical analysis of responses.

4.2.5 Influence of Positive Assortative Mating

In humans and in many other species there is a well-recognised tendency to choose mates on the basis that they exhibit similar traits to one's own – that is, 'like preferring like' leading to positive assortative mating (Buss & Barnes 1986; Andersson 1994). In humans, a wide range of characteristics including age, race, religion, social status, cognitive abilities and personality dispositions have been found to be subject to positive assortative mating (Buss & Barnes 1986). The possibility therefore existed that mate preference towards altruistic traits might simply be a reflection of a desire to choose a mate with the same degree of 'altruistic personality' as one's own. In analysis of data the effect of the subject's own 'altruistic personality' on mate preference towards altruistic traits will therefore be examined as this is relevant to the question of whether mate choice on the basis of altruistic traits is occurring.

4.2.6 The Questionnaire

A questionnaire was compiled including psychometric scales that measured mate preference towards altruistic traits, self-reported altruism, social desirability and other mate preferences (see Appendix 4.1). The first section of the questionnaire was entitled 'Mate Preferences' and asked subjects to rate each item on the basis of its relative desirability in a husband, wife or partner on a five-point Likert-type scale. To avoid the purpose of the MPAT scale becoming apparent the nine items were included at random with the 18 items of the GMP scale employed in Study 1. To match the style of the wording of the items in the MPAT scale, items in the GMP scale were changed so that they began with a verb (e.g. 'Dependable character' was replaced with 'Has a dependable character'). In one case the wording was seen as clearer by replacing 'Chastity – no previous experience of sexual intercourse' with simply 'Has no prior sexual experience'. As all items in the MPAT and GMP scales were expressed in a positive direction a number of negative items (e.g. 'Not bothered about being thought stingy towards other people') were also included from the list of items discarded in Study 1 to encourage subjects to think carefully about each response and not fall into a pattern of routinely ticking the same column (Oppenheim 1992). These negative items were not used in any further analysis.

The second section of the questionnaire assessed self-reported altruism, using the SRA scale, and was disguised under the heading 'Self-Assessment' (see Appendix 4.1). A number of minor changes to the wording of the SRA scale were made to reflect the different culture, context and time in which the scale would be used. The word 'photocopier' was substituted for 'Xerox machine', 'lift' for 'elevator' and 'give change for a banknote' for 'make change'. Also, the wording 'helped a classmate who I did not know that well with a homework assignment' was changed to give it relevance to the subjects in this sample (i.e. 'helped a workmate or classmate who I did not know that well with a task'). Finally, I judged that although the item 'helped push a stranger's car out of the snow' was very appropriate for the society in which the scale was first used (Canada), it would be less meaningful to subjects in this sample than 'helped push a stranger's car that had broken down'.

The SD scale was included in the questionnaire under the title ‘Personal Attitudes and Traits’ to avoid its purpose becoming apparent (see Appendix 4.1). A page requesting personal details including gender, whether the subject was a twin or spouse/partner, age, marital status, length of relationship if applicable and religion was also included (see Appendix 4.2). A covering letter was compiled in consultation with a representative of the Twin Research and Genetic Epidemiology Unit that explained the nature of the research to the twin and to the spouse/partner (see Appendix 4.3). Subjects were told that their responses would be treated in the strictest confidence. A consent form had been completed by the twins separately as part of the administrative arrangements for the ‘twin day’ but in the questionnaire to be completed by the spouse/partner they were asked to sign and date a statement that they had consented to take part in the study, which was added to the covering letter (see Appendix 4.3).

4.2.7 Processing of Data

Analysis was conducted using SPSS version 14.0. Occasionally subjects failed to respond to a particular item, which was a potential problem in that it could reduce statistical power across the sample as a whole. Substitution of missing items with the mean score of that subject for all other items in response to the scale in question is considered a reasonable solution to this problem (Oppenheim 1992: p.279-281) and is a practice that has often been used (Rushton & Bons 2005; Moore et al. 2006). However, it was decided to take a conservative approach to mean substitution in this study. In the case of the nine-item MPAT scale mean substitution took place where no more than one item was missing, in the case of the 20-item SRA scale where no more than two items were missing and in the case of the 33-item SD scale where no more than three items were missing. Mean substitutions calculated as a percentage of total potential items amounted to 0.36 % for the MPAT scale, 0.48 % for the SRA scale and 0.37 % for the SD scale.

4.2.8 The Problem of Pseudoreplication

Human mate choice usually involves two mating decisions made more or less simultaneously. When attempting to measure mate preference and preferred trait in two directions between spouses/partners, this raises the statistical problem of pseudoreplication. In data gathering, an easy mistake to make is to double-count, thus falsely inflating the value of *n* through pseudoreplication. To avoid this problem here, it was decided to divide the sample into two sub-samples – one in which the twin's MPAT score was compared with the spouse/partner's SRA score and one in which the spouse/partner's MPAT score was compared with the twin's SRA score. Thus Prediction1 was tested twice with two related but separate samples.

A further difficulty involving pseudoreplication concerned the use of twins in this study design. Twins share heredity and a common environment and so, to this extent, do not provide two independent sources of data. To circumvent this problem, the scores of twins were averaged and treated as a single source of data. The same was done for spouses/partners of twins.

4.2.9 Analysis of Covariance (ANCOVA)

Prediction 1 was tested using analysis of covariance (ANCOVA) in SPSS version 14.0 where the spouse/partner's SRA score was treated as the dependent variable, sex was a fixed factor and the focal individual's own MPAT, SRA, SD scores and age and length of relationship were treated as covariates. All possible two-way interactions were also fitted. These terms were systematically removed, starting with the least significant interaction until only significant terms remained in a 'minimum adequate' model. Results are presented for all main effects and for all significant interactions.

4.2.10 Further Testing of Reliability and Validity

As discussed in Chapter 3, testing reliability and validity is an ongoing process. The opportunity was therefore taken in this study to measure the MPAT scale's internal consistency and its construct validity. One would expect responses to a scale designed to measure mate preference towards altruistic traits to have some significant correlation with those in response to one designed to assess the construct of mate preference (i.e. the GMP scale, as discussed in Chapter 3) and the construct of 'altruistic personality' (as measured by the SRA scale). Construct validity was therefore assessed by correlation between responses to the MPAT scale and these other two scales.

The design of this study also offers a further test of the validity of the new scale. The scale's purpose is to measure mate preference towards altruistic traits and thus a key test of whether it performs that function is to measure whether degree of mate preference successfully ‘predicts’ degree of ‘altruistic personality’ in the mate actually chosen. Thus confirmation of Prediction1 would also support the validity of the new scale. Although not strictly predictive validity since it concerns mating decisions that occurred in the past, this nevertheless can be seen as offering a useful additional test of the MPAT scale’s validity.

4.2.11 How Desirable are Altruistic Traits?

If mate preference towards altruistic traits is linked to sexual selection we would expect individuals to rate altruistic traits as desirable and attractive in absolute terms. The mean score in response to the MPAT scale was thus compared using a one-sample t-test with the mid-point score of the MPAT scale. The mean MPAT score was also ranked alongside mate preferences towards the 18 items of the GMP scale to provide an indication of the relative desirability of altruistic traits in relation to a range of other characteristics in a mate.

4.3 Results

4.3.1 Characteristics of Sample

Among all subjects who attended the ‘twin days’ those who reported themselves as being married (*n* = 214) or living with a partner (*n* = 32) amounted to 68.72 % of the total. Of those who reported themselves as being in such long-term relationships 170 had spouses or partners who subsequently completed the questionnaire, a response rate of 69.12 %. The final sample of twins and their spouses/partners thus contained 340 subjects.

The demographic characteristics of the final sample can be found in Table 4.1. The mean age of subjects in this sample was almost three times the mean age of the sample found in Study 1, which was 19.4 years. While the student sample unsurprisingly exhibited a narrow age range (*s.d.* = 1.27 years) this sample had a much wider range (*s.d.* = 12.24 years), with ages ranging from 22 to 90 years.

It was presumed that those who reported themselves as single, divorced, widowed or undisclosed nevertheless saw themselves as being in a long-term relationship, even though they may not have been physically living with a partner. The two additional males in the sample were homosexual who were included in the analysis. The 13 subjects who reported themselves as not being heterosexual could be seen as bisexual but currently part of a heterosexual relationship. Compared with the sample in Study 1, this sample contained a higher percentage of those reporting themselves as being U.K. nationals and White European. This sample also contained a higher percentage of those who reported themselves as Anglicans and a smaller percentage to those who reported themselves as 'Agnostic/Atheist'.

Table 4.1. Demographic breakdown of subjects in Study 2

Category		Response (± standard error of mean)	Percentage Response
Gender:	Female	168	50.3
	Male	170	49.7
Mean Age	Years	57.9 (± s.e. 0.69)	
Marital Status	Single	7	2.1
	Married	285	84.6
	Divorced	4	1.2
	Living with Partner	40	11.9
	Widowed	1	
	Undisclosed	1	0.3
Length of Relationship	Years	29.94 (± s.e. 0.77)	
Would you describe yourself as heterosexual?	Yes	321	96.1
	No	13	3.9
	Undisclosed	4	
Are you a UK national?	Yes	336	99.4
	No	2	0.6
Ethnic Group	White European	329	98.8
	Other	4	1.2
Religion	Anglican	174	51.5
	Catholic	18	5.3
	Other Christian	63	18.6
	Agnostic/Atheist	60	17.8
	Jewish	6	1.8
	Other	17	5.0

4.3.2 Testing Prediction 1

A contrasting picture emerged between the two sub-samples used to test Prediciton1. There was a significant positive effect of the spouse/partner’s MPAT score on the twin’s SRA score (see sub-sample 2 in Table 4.3), thus confirming Prediction 1. But when this relationship was tested between the twin’s MPAT scores and the spouse/partners’ SRA scores a non-significant result was obtained (see sub-sample 1 in Table 4.2), thus not supporting Prediction1.

In sub-sample 1 (see Table 4.2) a significant but negative slope in the male data was found (slope parameter $B = -1.196$, $p < 0.001$) – that is, the stronger the mate preference the lower the degree of 'altruistic personality' found in the mate chosen. In contrast, in the female data a positive but narrowly non- significant slope was found ($B = 0.268$, $p = 0.054$) (see scatter plot in Figure 4.1).

A significant positive effect of the focal individual's SRA score on the spouse/partner's SRA score was found in both samples, thus indicating 'like preferring like', resulting in positive assortative mating on the basis of altruistic traits.

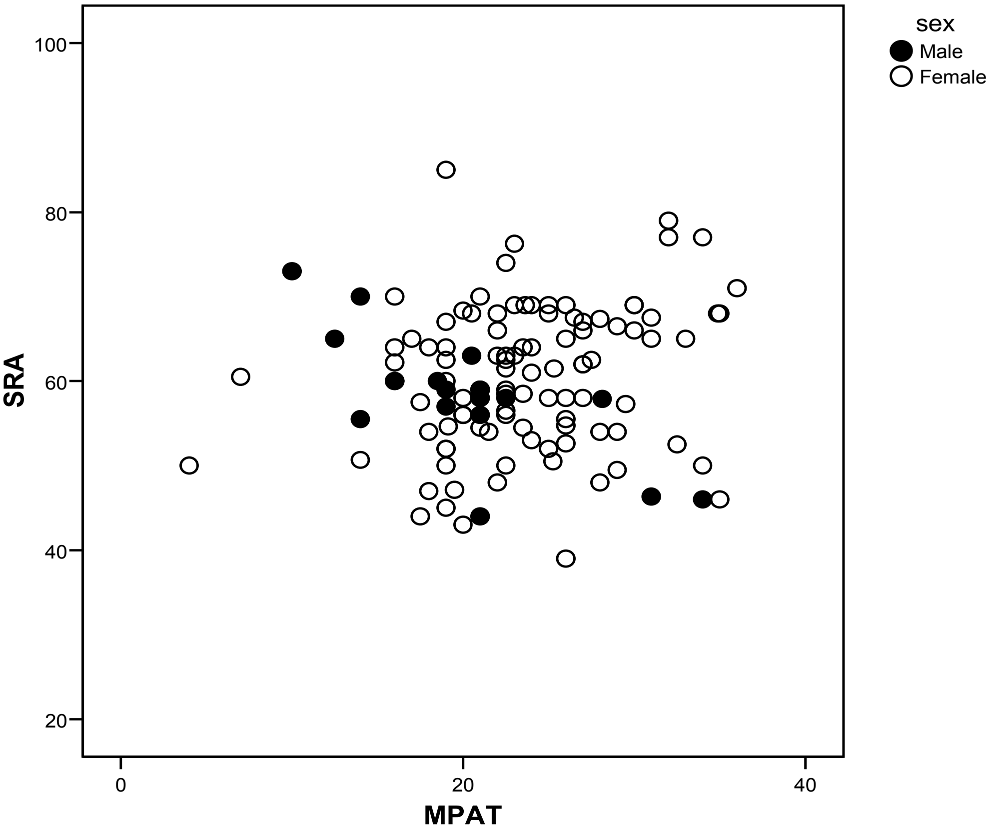
Table 4.2. Analysis of Covariance (ANCOVA) of Responses in Study 2: Sub-sample 1 (MPAT scores of twin in relation to SRA scores of the other spouse/partner)

Term	*df*	*F*	*p*
Sex	1,109	0.237	0.627
SRA	1,109	15.681	< 0.001
Length of Relationship	1,97	0.169	0.682
Age	1,108	0.078	0.781
SD	1,93	0.062	0.805
MPAT	1,109	1.233	0.269
Sex*MPAT	1,109	13.082	< 0.001

Table 4.3. Analysis of covariance (ANCOVA) of responses in Study 2: sub-sample 2 (MPAT scores of spouse/partner in relation to SRA scores of twin)

Term	*df*	*F*	*p*
Sex	1,79	1.537	0.219
SRA	1,102	8.376	0.005
Length of Relationship	1,102	10.514	0.002
Age	1,80	1.987	0.163
SD	1,77	0.081	0.777
MPAT	1,102	5.704	0.019

Figure 4.1. Scatter plot contrasting male and female MPAT scores of twins in relation to their spouses' SRA scores (sub-sample 1)



4.3.3 Reliability and Validity

The internal consistency of the MPAT scale was found to be high (α = 0.84) and the same was true of the three other scales employed in this study (α = 0.82). In terms of construct validity, the correlations with responses to the GMP and SRA scales indicated that the MPAT scale significantly assessed the constructs of mate preference (Pearson correlation: $r_{293} = 0.36$, $p = < 0.001$) and 'altruistic personality' (Pearson correlation: $r_{324} = 0.17$, $p = 0.003$).

4.3.4 Relative Strength of Mate Preference towards Altruistic Traits

The mean MPAT score was 21.96 which was found to be significantly higher than the mid-point score of 18.5 (one-sample t-test: $t_{328} = 9.83$, $p < 0.001$). The mean MPAT score was then ranked alongside items from the GMP scale and was ranked 17th out of a possible 19 items (see Table 4.3).

Table 4.3. Ranking of Mean Scores in Response to MPAT Scale and Items of GMP Scale in Study 3

Items	**Mean Scores (± standard error of mean)**
There is mutual attraction – love	3.78 (± 0.048)
Has a dependable character	3.76 (± 0.031)
Has a pleasing disposition	3.51 (± 0.036)
Shows emotional stability and maturity	3.46 (± 0.038)
Has a desire for home and children	3.33 (± 0.048
Is sociable	3.31 (± 0.040)
Enjoys good health	3.30 (± 0.046)
Has education and intelligence	3.19 (± 0.048)
Shows refinement and neatness	2.87 (± 0.048)
Is a good cook and housekeeper	2.81 (± 0.051)
Has a similar education to me	2.76 (± 0.057)
Is ambitious and industrious	2.66 (± 0.051)
Has a similar religious background to me	2.65 (± 0.065)
Is good looking	2.61 (± 0.050)
Has good financial prospects	2.51 (± 0.052)
Has a favourable social status or rating	2.47 (± 0.055)
MPAT Mean	2.44 (± 0.039)
Has a similar political background to me	2.42 (± 0.055)
Has no prior sexual experience	1.86 (± 0.064)

4.4 Discussion

Mate preference towards altruistic traits (MPAT scores) was significantly correlated with the desired degree of ‘altruistic personality’ (SRA scores) in the mate chosen in one sub-sample but not in the other. In the other sub-sample the puzzling negative slope in the relatively small male data contrasted with a result for females that was more consistent with the prediction being tested. The negative slope in the male data in sub-sample 1 is difficult to interpret. In effect, the greater the desire for an altruistic mate the lesser the degree of ‘altruistic personality’ found in the mate chosen. There is no evidence of systematic differences in personality traits between twins and others (Johnson et al 2002) and yet it is possible that the mate preference towards altruistic traits of male twins is untypical due to some unknown cause. This effect was, however, not found in the other sub-sample. Use of this design in a further study using a sample of spouses and partners who are not twins may throw light on this puzzling result.

One firm conclusion from these results was that there was a significant relationship between subjects’ own SRA score and their spouse/partners’ SRA score in both samples. This indicated that ‘like preferring like’ on the basis of ‘altruistic personality’ was present in this sample, leading to positive assortative mating on these traits. Altruism can thus be seen as one of a number of human characteristics subject to this process (Buss & Barnes 1986). This result therefore provides evidence that mate choice on the basis of altruistic traits is taking place in modern populations.

Age and length of relationship were strongly correlated in sub-sample 2, which is scarcely surprising. In this sub-sample a positive relationship between length of relationship and spouse/partner's SRA score was found. This may well be an effect of a tendency for responses to all scales to become more positive as age increases – a point that will be discussed in more detail in Chapter 5 (see Section 5.4). This confounding variable would be reduced if, as discussed in Section 4.2.4, mate choice on the basis of altruistic traits could be measured when mate choice is being made.

This study provided the first substantial support in favour of the validity of the MPAT scale. The new scale was found to significantly and positively assess the constructs of mate preference and 'altruistic personality' - as a scale designed to measure mate preference towards altruistic traits should be expected to. As well as supporting the construct validity of the MPAT scale, the new scale demonstrated its ability to 'predict' the desired degree of 'altruistic personality' in the mate chosen in one sub-sample. To the extent that Prediction 1 was supported the validity of the new scale was therefore also confirmed. The reliability of the MPAT scale, as evidenced by its internal consistency, continued to be good.

Mate preference towards altruistic traits was expressed in a significantly positive direction. I therefore conclude that subjects found altruistic traits desirable in absolute terms in a mate, a finding consistent with the sexual selection hypothesis. The relatively low rating of mate preference towards altruistic traits compared with those characteristics in the GMP scale may well be a reflection of these other characteristics incurring no obvious fitness cost (e.g. 'good looks', 'ambitious and industrious’, ‘good financial prospects’). The fitness cost of mate preference towards altruistic traits has been discussed in Section 2.7.3 and may account for this result.

To sum up, Prediction 1 was supported in one sub-sample while a suggestive relationship between mate preference and preferred trait in the mate chosen was found in the other. Mate choice in terms of ‘like preferring like’ on the basis of ‘altruistic personality’ was demonstrated in both sub-samples. The inference can be drawn that there is encouraging evidence for mate choice on the basis of altruistic traits in a modern population but that further research is required to confirm this predicted pattern.

4.5 Summary

- A significant relationship between degree of mate preference towards altruistic traits in one spouse/partner and desired degree of 'altruistic personality' in the other was found in one sub-sample.
- Positive assortative mating on the basis of 'altruistic personality' was demonstrated in both sub-samples.
- The validity of the MPAT scale were supported by it significantly assessing the constructs of mate preference and 'altruistic personality' and by it successfully 'predicting' the desired degree of 'altruistic personality' in the mate chosen. Its internal consistency continued to be good.
- Responses to the MPAT scale were expressed in a significantly positive direction.
- Further research is required to test Prediction 1, employing a larger and completely random sample ideally containing subjects who are about to or have just made a mate choice.

CHAPTER 5. SEX DIFFERENCES IN MATE PREFERENCE TOWARDS ALTRUISTIC TRAITS (STUDY 3)

5.1 Introduction

5.1.1 Sex Differences in Mate Preference towards Altruistic Traits

Sexual selection is typically seen as a process that results in sexually selected traits being expressed prominently in one sex but either not at all or in a truncated form in the other (Darwin 1871). In Chapter 2 (Section 2.2) various models were discussed that seek to account for differences commonly found between the sexes in mate preference and preferred traits (Bateman 1948; Trivers 1972; Emlen & Oring 1977; Clutton-Brock & Vincent 1991; Kokko & Monaghan 2001; Kokko & Johnstone 2002; Wade & Shuster 2002; Arnqvist & Rowe 2005; Simmons & Kvarnemo 2006). The genetic mechanisms by which sex differences emerge over evolutionary time as a result of differing selection pressures acting on males and females have also been clarified in theoretical models (e.g. Lande 1981).

In Chapter 2 (Section 2.7) it was proposed that the expansion of the human brain could have led to the need for increasing parental investment. In the scenario presented, it was suggested that this could have led to intense selection pressure acting on females hominids to identify and choose mates who would be willing as well as able to provide sustained and long-term resources and protection for the female and her offspring. If displays of altruism towards non-kin had correlated with a subsequent willingness and ability to provide such parental investment then genes associated with human altruism towards non-kin could have been favoured – along with the mate preference towards such traits.

Contemporary mate preferences can provide important clues to human reproductive evolution (Buss 1989) as, under intersexual selection mechanisms (Andersson & Simmons 2006), the mate preference is subject to genetic influence. Thus any sex differences in mate preference as a result of past selection pressure is likely to be reflected, in some form, in modern populations. A psychometric scale was therefore developed, as reported in Chapter 3, to measure mate preference towards altruistic traits (the MPAT scale). A key test of whether contemporary mate preference towards altruistic traits is consistent with the scenario discussed in Section 2.7 is therefore whether a significantly stronger female mate preference, as measured by the MPAT scale, emerged.

Study 1 (as reported in Chapter 3) could not satisfactorily measure sex differences in mate preference as subjects may not have been blind to the prediction being tested. It was essential that the MPAT scale be employed as part of an appropriate study design in which items were included at random among other more general mate preferences to disguise the purpose of the study. Sex differences in mate preference towards altruistic traits might also be influenced by a tendency to give socially desirable responses and the 'altruistic personality' of the subject leading to 'like preferring like' (see Chapter 4). It was therefore essential that the SD and SRA scales, absent in Study 1, be included in an appropriate study design. Furthermore, Study 1 was needed to compute the minimum sample size needed in Study 3, given the effect size being studied and the need for adequate statistical power. Inadequate sample size also precluded use of the data in Study 2 to detect sex differences in mate preference towards altruistic traits, although the opportunity will be taken to investigate any suggestive tends in that study also. For all these reasons, a new study was essential and so in Study 3 I set out to test the following prediction:

Prediction 2: A significantly stronger female mate preference towards altruistic traits, as measured by the MPAT scale, will be found after the effects of social desirability and 'altruistic personality, as measured by the SD and SRA scales, have been taken into account.

5.2 Methods

5.2.1 Sample Size

The method specified by Cohen (1992) was used to carry out statistical power analysis of the data in Study 1 to estimate the minimum sample size needed for Study 3. Statistical power is about calculating the probability of correctly rejecting a false null hypothesis (Cohen 1992). The first objective was to obtain an approximate estimate of the mean effect size of any difference between female and male responses to the nine items of the MPAT scale in Study 1. This is indicated by the statistic d (obtained by subtracting the male mean score from the female mean score for each item and dividing by the pooled standard deviation) (see Table 5.1).

Table 5.1. Calculation of effect size of sex differences between independent means in response to MPAT scale (based on data from Study 1)

Item	***d***
Volunteered to help out in a local hospital	0.130
Volunteered to help without pay on a week's holiday for disabled people	0.216
Regularly helps an elderly neighbour	0.264
Ran the London Marathon to raise money for a good cause	0.083
Once dived into a river to save someone from drowning	0.129
Donates blood regularly	0.346
Climbed a tree to rescue a neighbour's cat	0.234
Once cared for a stray dog injured by a car	0.307
Helped clear people away from a suspect package found in an airport	0.077
Mean for MPAT Scale (*d*) =	**0.198**

This resulted in a mean value of *d* for the MPAT scale, which was very close to Cohen's definition of a small effect size ($d = 0.20$) (Cohen 1992). Given significance at 0.05 (two-tailed) and a value for power of 0.80, this indicated a minimum sample size of 393 (Cohen 1992). As the sample size obtained in Study 1 ($n = 380$) involved four halls of residence this seemed an appropriate number to approach initially, with the option of visiting a fifth should the sample fall short of the minimum size required.

5.2.2 The Sample

Permission was obtained to carry out surveys in four halls of residence at the University of Nottingham and these took place during April and May 2005. The approach taken was the same as that described in Study 1 and a similarly positive response from subjects was found. Subjects were told that they were taking part in a study of their mate preferences and other characteristics. No mention was made of altruistic traits.

5.2.3 The Questionnaire

A questionnaire containing the MPAT, SRA, SD and GMP scales was compiled on a similar basis to that employed in Study 2 (see Appendix 4.1). However, the page requesting demographic details used reflected that employed in Study 1 (see Appendix 3.2). The consent form (see Appendix 3.3) was kept separate, as in Study 1, so as to preserve the confidentiality of the subject.

5.2.4 Processing of Data

The data were analysed using SPSS version 14.0. Subjects occasionally failed to respond to a particular item, as reported in Chapter 4, and, to avoid a reduction in the statistical power of the sample, substitution with the mean score for all other items in a scale was employed for missing data (Oppenheim 1992: p.279-281). The same conservative approach as in Chapter 4 was employed with mean substitutions calculated as a percentage of total potential items amounting to 0.36 % for the MPAT scale, 0.48 % for the SRA scale and 0.37 % for the SD scale.

5.2.5 Testing Sex Differences in Response to MPAT Scale in Study 3

Analysis of covariance (ANCOVA) was employed with MPAT scores as the dependent variable, sex as the fixed factor and SRA and SD scores as covariates. As the standardised residuals were not normally distributed the MPAT data were transformed by squaring them and the ANCOVA re-run. Homogeneity of variances and normality of residuals were found to be satisfactory throughout. All possible two-way interactions were fitted and these terms systematically removed, starting with the least significant interaction until only significant terms remained in a 'minimum adequate' model.

5.2.6 Testing Sex Differences in Response to MPAT Scale in Other Studies

Sex differences in response to the MPAT scale were also examined in samples obtained in other studies. These samples, however, offer a less satisfactory test of Prediction 2 than that provided by Study 3, for various reasons (see Section 5.1.1). The adjusted twin (n = 180) and spouse/partner (n = 122) samples both fell far short of the sample size required for adequate statistical power (n = 393). These results were, however, examined to see whether any suggestive patterns emerged but were treated with corresponding caution. In the case of the twin and spouse/partner data this raised the question of pseudoreplication since the twins share a common environment and heredity, and their spouse/partners are also not independent sources of data. Mean scores were therefore computed for each twin pair and pair of spouse/partners to eliminate pseudoreplication.

5.2.7 Other Tests of Data

An alternative explanation for any sex differences found in response might be that the sexes in this sample differed in how positively they respond to psychometric scales in general. Thus a stronger female mate preference towards altruistic traits might simply reflect a more positive female response to the process of completing psychometric scales in these samples. To deal with this possibility, responses to the SRA, SD and GMP scales were also examined. Other patterns in the data were examined in the light of what was revealed by the results.

Finally, the opportunity was taken to retest the reliability and validity of the MPAT scales here in Study 3. The degree to which subjects found altruistic traits relatively desirable was also re-examined using the two approaches employed in Study 2.

5.3 Results

5.3.1 Characteristics of the Sample

The number of subjects who completed the questionnaire (*n* = 398) just exceeded the sample size required to achieve adequate statistical power (*n* = 393). The mean age of the sample was exactly the same as that obtained in Study 1 with only a slightly different standard deviation (*s.d.* = 1.93). The demographic characteristics of this sample can be found in Table 5.2. They were found to be very similar to those found in the other student sample reported in Study 1.

Table 5.2. Demographic breakdown of subjects in Study 3

Category		**Response**	**%age Response**
Gender	Female	187	47.0
	Male	211	53.0
Mean Age	Years (± s.e.)	19.41 (± 0.10)	
Marital Status	Single	388	97.5
	Married	1	0.3
	Divorced	2	0.5
	Living with Partner	5	1.26
	Widowed	1	0.3
	Undisclosed	1	0.3
Are you currently in a close relationship?	Yes	139	34.9
	No	239	60.1
Would you describe yourself as heterosexual?	Yes	385	96.7
	No	13	3.3
Are you a UK national?	Yes	356	89.4
	No	41	10.3
	Undisclosed	1	
Ethnic Group	White European	338	84.9
	African	3	0.8
	Bangladeshi	3	0.8
	Indian	7	1.8
	Pakistani	1	0.3
	Other Asian	23	5.8
	Other	22	5.5
	Undisclosed	1	
Religion	Anglican	77	19.3
	Catholic	43	10.8
	Other Christian	84	21.1
	Agnostic/Atheist	134	33.7
	Buddhist	7	1.8
	Hindu	5	1.3
	Islam	11	2.8
	Jewish	7	1.8
	Sikh	1	0.3
	Other	22	5.5
	Undisclosed	7	

5.3.2 Testing Prediction 2

The mean female score in response to the MPAT scale in Study 3 was 21.24 (± s.e. 0.384) and the male score 20.04 (± s.e. 0.332). When the ANCOVA was run this sex difference was found to be significant (see Table 5.3), thus supporting Prediction 2.

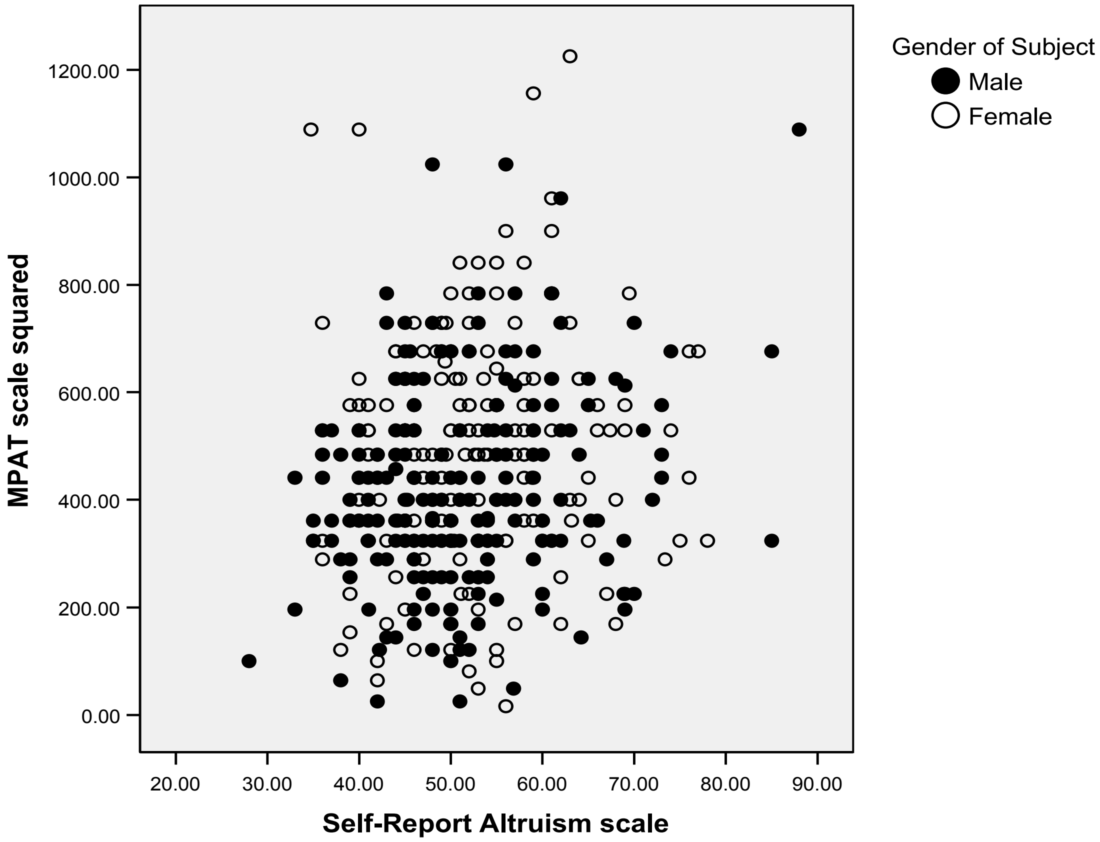
Table 5.3. Analysis of covariance (ANCOVA) of responses in Study 3 (*n* = 398).

Term	*F (df)*	*p*
SRA*	10.481 (1,387)	0.001
SD	2.541 (1,380)	0.112
Sex*	6.547 (1,387)	0.011

Note: * indicates terms in minimum adequate model

Responses to the SRA scale had a significant effect on MPAT scale scores and the positive relationship between responses to the two scales is illustrated in Figure 5.1.

Figure 5.1 Student sample (Study 3): scatter plot of relationship between MPAT and SRA scores



5.3.3 Sex Differences in Response to MPAT scale in Other Studies

Mean female MPAT scores were found to be higher than male scores in all three other samples (see Table 5.4). A significantly stronger female response was found in the twin sample (see Table 5.5) and in Study 1 (analysis of variance: $F_{1,\,368} = 8.96$; $p = 0.003$) but in the spouse/partner sample no main effect had any significant relationship with MPAT score (see Table 5.6).

Table 5.4. Sex differences in response to MPAT scale in other studies

	Mean Scores (± standard error of mean)	
	Female	Male
Study 1	23.81 (± 0.305)	22.505 (± 0.312)
Twin Sample (Study 4)	23.53 (± 0.397)	20.75 (± 1.099)
Spouse/ Partner Sample (Study 2)	22.14 (± 1.642)	20.63 (±0.542)

Table 5.5 Analysis of covariance (ANCOVA) of responses to the MPAT scale in the adjusted twin sample (*n* = 180).

Term	*F (df)*	*p*
SRA	3.100 (1,175)	0.080
Age*	5.144 (1,177)	0.025
SD	0.746 (1,171)	0.389
Sex*	6.289 (1,177)	0.013

Note: * indicates terms in minimum adequate model

Table 5.6. Analysis of covariance (ANCOVA) of responses to the MPAT scale in the adjusted in spouse/partner sample (n = 122).

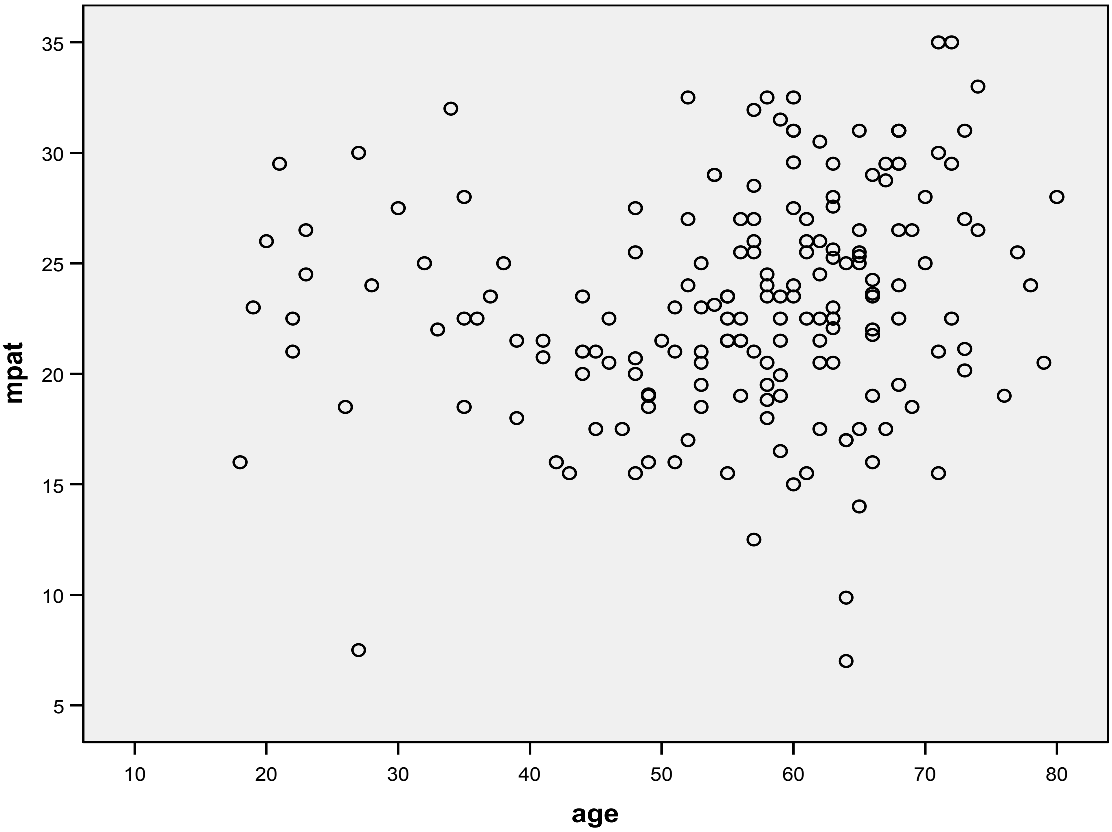
Term	*F (df)*	*p*
SRA	8.376 (1,112)	0.094
Age	1.987 (1,87)	0.906
SD	0.081 (1,109)	0.533
Sex	1.537 (1,111)	0.204

Note: the minimum adequate model included none of the effects of interest, just an intercept.

5.3.4. Age and Responses to MPAT Scale

It can be seen from the ANCOVA model of the adjusted twin sample (see Table 5.5) that age as well as sex had a significant effect on the dependent variable, MPAT scale scores. A pattern of age correlating positively with responses to other scales was also found (SRA scale $r_{179} = 0.28$, $p < 0.001$; SD scale $r_{177} = 0.25$; $p = 0.001$). The tendency for older subjects to respond more positively to the MPAT scale is illustrated in Figure 5.2.

Figure 5.2 Twin sample (Study 4): scatter plot of relationship between MPAT scores and age



Closer examination of this association suggested a U-shaped rather than linear relationship between age and MPAT scale scores with subjects in the 20-30 year age range expressing a stronger preference than those in the 40-50 year age range. It may be logical that younger subjects of reproductive age expressed a stronger mate preference compared with more middle-aged subjects. In statistical terms, the association between age and MPAT score could well be modelled more effectively with a quadratic rather than a linear relationship. A new ANCOVA was therefore run which included a quadratic term (see Table 5.7). In the new analysis the age^2 term was significant (with a parameter estimate of 0.007), as were the effects of SRA score and sex. The addition of the quadratic term improved the fit of the model from R^2 = 0.078 in the original model to R^2 = 0.107 in the new.

Table 5.7. Analysis of covariance (ANCOVA) of responses to the MPAT scale in adjusted twin sample (n = 180) with quadratic relationship between age and MPAT score.

Term	*F (df)*	*p*
SRA	4.282 (1,172)	0.040
Age	2.703 (1,171)	0.102
SD	0.730 (1,170)	0.394
Age^2	4.419 (1,172)	0.037
Sex	6.823 (1,172)	0.010

Variance in age was, understandably, not an important feature of the student sample when compared with the twin sample (student sample: mean age = 19.4 ± s.e. = 0.097; adjusted twin sample: mean age = 55.94 ± s.e. = 0.997) although variation in age was prominent in the spouse/partner sample (mean age = 57.31 ± s.e. = 1.298). The same method was therefore applied to the spouse/partner sample. The effect of age^2 was found to be significant (parameter estimate: 0.008). Interestingly, SRA score demonstrated a significant effect on MPAT score in the new analysis (see Table 5.8), in contrast with the absence of any significant association when only a linear relationship with age was fitted.

Table 5.8. Analysis of covariance (ANCOVA) of responses to the MPAT scale in the adjusted in spouse/partner sample (*n* = 122) with quadratic relationship between age and MPAT score.

Term	*F (df)*	*p*
SRA	4.732 (1,90)	0.032
Age	0.054 (1,86)	0.817
SD	0.578 (1,89)	0.449
Age^2	0.021 (1,87)	0.884
Sex	0.448 (1,88)	0.505

5.3.5 Sex Differences in Response to SRA, SD and GMP Scales in Study 3

To check whether a common pattern of more positive female response to psychometric scales might account for confirmation of Prediction 2, sex differences in response to the other three scales used in Study 3 were examined (see Table 5.9). However, no significant sex difference was found, thus eliminating this possible explanation.

Table 5.9. Study 3: Mean scores by sex of responses to other scales used and analysis of variation (ANOVA) of differences

	Mean Scores (± standard error of mean)		
	Female	Male	Sex Difference (*F* and *p* values)
SRA	52.84 (± 0.66)	51.06 (± 0.70)	$F_{1,389} = 3.36$; $p = 0.068$
SD	14.01 (± 0.37)	13.48 (± 0.34)	$F_{1,386} = 1.07$; $p = 0.301$
GMP	51.42 (± 0.47)	50.43 (± 0.43)	$F_{1,376} = 2.42$; $p = 0.120$

The absence of any significant sex difference in SRA score was noteworthy in that 'altruistic personality' was treated as the preferred trait. One might thus expect a significant sex difference in response here also on the basis of sexual selection theory, as discussed in the Introduction. Sex differences in response to the SRA scale in the other samples were therefore examined (see Table 5.10) but no significant sex differences between scores were found there either.

Table 5.10. Mean scores and analysis of variation (ANOVA) of sex differences in response to SRA scales in adjusted twin and spouse/partner samples.

	Mean Scores (± standard error of mean)		
	Female	Male	Sex Difference (F and p values)
Twin sample	60.81 (± 0.683)	63.47 (± 2.185)	$F_{1,177} = 1.65; p = 0.201$
Spouse/partner sample	57.36 (± 1.814)	60.37 (± 0.855)	$F_{1,117} = 1.74; p = 0.190$

5.3.6 Reliability and Validity

The internal consistency of the MPAT scale in this study was found to be $\alpha = 0.83$ while that of the three other scales was $\alpha = 0.81$ (SRA scale), $\alpha = 0.72$ (GMP scale) and $\alpha = 0.74$ (SD scale). In terms of construct validity, the correlations with responses to the GMP and SRA scales indicated that the MPAT scale significantly assessed the constructs of mate preference ($r_{377} = 0.35$, $p = < 0.001$) and ‘altruistic personality’ ($r_{390} = 0.16$, $p = 0.003$).

5.3.7 Relative Strength of Mate Preference towards Altruistic Traits

A one-sample t-test was employed, using the mid-point of the range between the minimum and maximum scores in response to the MPAT scale (i.e. 18.5). The actual mean MPAT score for Study 3 was 20.60, which was found to be significantly higher than the mid-point score using a one-sample t-test ($t_{396} = 8.31$, $p < 0.001$). Compared with the range of characteristics in the GMP scale the mean response to the MPAT scale was ranked 16th out of a possible 19 items (see Table 5.11).

Table 5.11. Ranking of mean scores in response to MPAT scale and items of GMP scale in Study 3

Items	Mean Scores (± standard error of mean)
There is mutual attraction – love	3.79 (± 0.027)
Is sociable	3.41 (± 0.033)
Has education and intelligence	3.39 (± 0.035)
Shows emotional stability and maturity	3.22 (± 0.036)
Has a dependable character	3.19 (± 0.044)
Is good looking	3.19 (± 0.038)
Has a desire for home and children	3.00 (± 0.050)
Enjoys good health	2.99 (± 0.039)
Has a pleasing disposition	2.98 (± 0.039)
Is ambitious and industrious	2.85 (± 0.040)
Is a good cook and housekeeper	2.77 (± 0.041)
Has a similar education to me	2.65 (± 0.043)
Has good financial prospects	2.62 (± 0.044)
Has a favourable social status or rating	2.42 (± 0.044)
Shows refinement and neatness	2.36 (± 0.045)
MPAT Mean	***2.29(± 0.029)***
Has a similar religious background to me	2.24 (± 0.053)
Has a similar political background to me	2.07 (± 0.043)
Has no prior sexual experience	1.82 (± 0.050)

5.4 Discussion

A significantly stronger female mate preference towards altruistic traits, as measured by the MPAT scale, was found in Study 3, thus confirming Prediction 2. This result is thus consistent with scenario proposed in Chapter 2 and the sexual selection hypothesis for the evolution of human altruistic traits.

Other samples in this thesis where this sex difference was measured either lacked adequate statistical power and/or had weaknesses in their study design for this purpose. Nevertheless a higher female MPAT score was found in all three samples of substantially different mean age, a result that was significant in two of the three samples. Qualified support can therefore also be found in these other samples for a stronger female mate preference towards altruistic traits, although replication of these results is required in samples of sufficient statistical power and suitable design.

It is possible to interpret the stronger female mate preference towards altruistic traits found here as not being linked to sexual selection but solely as a response by females to the particular social environment that they inhabit. For example, under the ‘social role theory of gender’ (Eagly & Crowley 1986) social norms are seen as favouring a ‘nurturant and caring’ role for females. It may thus be that females disproportionately looked for mates who will help them in this role. Another possible interpretation could be based on the ‘structural powerlessness’ model (e.g. Wallen 1989, Moore et al 2006) where females are seen as having relatively limited access to power and resources. In this environment, signs of a willingness to share power and resources, as evidenced by altruistic behaviour in a mate, might account for the stronger female mate preference found. The relative effects of genotype and environment on mate preference towards altruistic traits and ‘altruistic personality’ will be examined in Chapter 6. That study should therefore provide an insight into how much reliance can be placed on purely environmental interpretations of the stronger female mate preference found in this study.

A positive relationship was found between MPAT and SRA scores, suggesting that the degree of mate preference towards altruistic traits of the subject was being influenced by her/his degree of ‘altruistic personality’ or vice versa. This is perhaps not surprising in that ‘like preferring like’ has been noted as common pattern in human mating behaviour (Buss & Barnes 1986) and in other species (Andersson

1994). In Chapter 4 evidence for the subject's own SRA score being significantly related to that of the SRA score of the chosen spouse/partner was presented. The evidence here suggests that a pathway that includes mate preference towards altruistic traits completes the process although in this situation it is impossible to establish cause and effect.

The notion that the stronger female response found may simply have been a reflection of a generally more positive female response to all the psychometric scales used in these studies was contradicted by the absence of significant sex differences in response found in relation to other scales employed in this study. However, this then raises the question of why the preferred trait – 'altruistic personality' as measured by the SRA scale - does not conform to the typical pattern of a sexually selected trait. Classic sexual selection theory envisages sex differences in mate preference leading to sexual dimorphism in expression of the preferred trait (e.g. Lande 1981). Yet no significant sex difference in the preferred trait was found to match the significant sex difference in mate preference found here.

The literature is somewhat divided as to whether, in practice, any consistent sex differences in altruistic or related behaviour are displayed by humans. For example, Eagly and Crowley's (1986) meta-analysis of 99 studies of 'helping behaviour' found that males 'helped' significantly more frequently than females. This pattern was also reported elsewhere (Latané 1970; Kleinke 1977; Kleinke et al 1978; Goldberg 1995) although other studies (Krebs 1970; Rushton et al 1986: Table 2, p. 1194) have reported no such sex difference in altruistic behaviour and there is also a perception that females comprise the majority of those who perform voluntary activity (e.g. Henderson 1983), a view supported in Chapter 7. A study of female and male ‘heroic’ behaviour (Becker & Eagly 2004) found that females were at least as likely as males to put their lives at risk to help Jews during the Holocaust although males predominated in situations recognised by the Carnegie Hero Medal in North America, where physical prowess, immediate action and public surveillance were involved. It is thus difficult to draw a clear inference as to whether one sex or the other typically displays more altruistic behaviour or in which contexts this may be more likely.

A number of points may account for the absence of a significant sex difference in the preferred trait found in this study. Classic sexual selection theory envisages a rapid, almost parallel evolution of the preferred trait in males and females (Fisher 1915, 1958; Lande 1981, 1987). This is followed, in females, by the slow reduction in expression of the preferred trait, leading to sexual dimorphism, as its cost to viability under natural selection acts against its continued expression. In males, the preferred trait is subject to the opposing selective forces of reproductive success under sexual selection and cost to viability under natural selection until an equilibrium is reached (Lande 1981, 1987). As a result, sexual dimorphism in the preferred trait evolves. This process is, however, likely to be very gradual and take a long period of evolutionary time before it is complete (Lande 1987). What is seen in these results may thus simply reflect an intermediate evolutionary stage.

Alternatively, the scenario proposed in Chapter 2 under which human altruism towards non-kin might have been favoured could be very relevant here. It was suggested that a process of more equal parental investment between the sexes is likely to have developed during human evolution. On the basis of Trivers' (1972, 1985) theory this could have resulted in a form of mutual sexual selection, with sexual selection subsequently acting on the preferred trait in both sexes. This could have further slowed or even reversed the process by which sexual dimorphism in the preferred trait developed (Lande 1981, 1987).

Another possible explanation is that the SRA scale was insufficiently sensitive in measuring the altruistic behaviour of the subjects. Thus the methodology may have failed to recognise significant sex differences that were present. This explanation appears unlikely in view of the evidence for the reliability and validity of the scale discussed in Chapter 4.

The absence of any sex difference in response to the SRA scale therefore need not necessarily contradict the sexual selection hypothesis. However, the scenario presented in Chapter 2 is no more than a verbal outline and requires further development in the form of a theoretical model. Only then can the suppositions contained in it be subjected to rigorous examination, although the difficulties of quantifying parental investment (Knapton 1984) may well present serious problems. Until that takes place the sexual selection hypothesis must be treated with due caution.

The positive relationship found between age and responses to the MPAT and other scales employed is puzzling in that one might expect those of reproductive age to express the strongest mate preference. It is possible to speculate that older subjects may have been more influenced by a greater tendency to give a socially desirable response than younger subjects as a result of their being raised in a more deferential culture. Also, the SRA scale asks subjects to report the frequency with which they have carried out altruistic acts in the past and so, other things being equal, will have more opportunity to perform these altruistic acts. Older subjects should therefore score more highly than younger subjects for an equivalent level of 'altruistic personality'. Finally, it may be that, through selection as a result of volunteering to attend 'twin days', subjects were recruited who were more likely to give positive responses in completing the questionnaires. Whatever variables may explain this pattern, age and age-related variables need to be controlled for in future study designs that test the sexual selection hypothesis.

Finally, the construct validity of the MPAT scale was reinforced by the fact that, once again, it significantly assessed the constructs of mate preference and 'altruistic personality'. Correlations were very similar to those reported in Chapter 4 (see Section 4.3.3) which had samples of substantially different mean age, thus suggesting that this construct validity is robust. The reliability of the new scale was again confirmed by sound internal consistency being found.

5.5 Summary

- A significantly stronger female mate preference towards altruistic traits, as measured by the MPAT scale, was found in Study 3, thus confirming Prediction 2.
- Similar significant sex differences in response were found in two other samples, although these lacked adequate statistical power and a suitable study design for this purpose.
- An absence of significant sex difference in the preferred trait – ‘altruistic personality’ as measured by the SRA scale - was found. Possible explanations for this apparent anomaly were discussed.
- A positive relationship between MPAT and SRA scores was found, suggesting that mate preference towards altruistic traits was influenced by the ‘altruistic personality’ of the subject.
- A positive relationship between age and responses to the psychometric scales used indicates that age must be controlled for in future studies.
- Further research is required to replicate these results and to model formally the scenario proposed in Chapter 2.

CHAPTER 6. GENETIC INFLUENCE ON MATE PREFERENCE AND PREFERRED TRAIT (STUDY 4)

6.1 Introduction

6.1.1 Sexual Selection Mechanisms

As discussed in previous Introductions, the sexual selection hypothesis is based on intersexual selection acting on altruistic traits. A number of mechanisms have been proposed to account for how intersexual selection works (Andersson1994; Andersson & Simmons 2006):

- *Indicator mechanisms* (Zahavi 1975, Hamilton & Zuk 1982). The preferred trait reflects an individual's condition and viability to potential mates (Andersson 1994). In so far as the resulting mate choice selects 'good genes' the offspring will enjoy enhanced fitness.
- *Direct phenotypic effects* (Kirkpatrick & Ryan 1991; Ryan 1998). The usually female mate preference towards a male trait correlates with that mate's ability to provide material resources and protection to the female and her offspring;
- *'Runaway' selection* (Fisher 1915, 1958). Alleles associated with the mate preference and the preferred trait become genetically correlated leading to self-reinforcing co-evolution;
- *Sensory bias* (Endler & Basolo 1998; Ryan 1998; Boughman 2002). Female preference towards a male trait evolves initially under natural selection but with sexual selection subsequently evolving to exploit this bias;

- *Genetic Compatibility* (Trivers 1972; Mays & Hill 2004). Preference for a mate with alleles that complement the genome of the individual who exercises the mate choice promotes the fitness of the resulting offspring.

6.1.2 The Implications of these Sexual Selection Mechanisms for the Evolution of Human Altruistic Traits

In Chapter 2 (Section 2.3) how altruistic traits might have evolved under each of these sexual selection mechanisms was discussed:

- *Indicator mechanisms.* Where altruistic traits reveal underlying phenotypic and genetic quality to potential mates, most notably through successfully overcoming the 'handicaps' posed by those altruistic traits;

- *Direct phenotypic effects.* Where altruistic traits provide an accurate index of future willingness as well as an ability to provide long-term resources and protection to a mate and her offspring selection on mate preference towards those traits would take place in favour of altruism towards non-kin;

- *'Runaway' selection.* Genetic correlation between mate preference towards altruistic traits and the altruistic traits themselves could have led to self-reinforcing co-evolution in favour of these traits;

- *Sensory bias mechanism.* Altruistic behaviour towards close relatives (Hamilton 1963) could have created a sensory bias in females that might have been exploited by males in displays of altruism towards non-kin.

- *Genetic compatibility mechanism.* In an environment where both selfish and altruistic genes offer selective advantages in different contexts it may have been beneficial for offspring to carry genes associated with both strategies.

6.1.3 Heritability of Mate Preference Consistent with Sexual Selection Acting on the Trait of Interest

In this study the initial assumption made is that, for the intersexual selection mechanisms discussed above to operate, variation in the mate preference must be under genetic influence (i.e. it must be heritable). In reviewing these mechanisms Andersson and Simmons (2006) emphasised that:

> ‘The evolution of mate choice is based either on direct selection of a preference that gives a fitness advantage…or on indirect selection of a preference as it becomes genetically correlated with directly selected traits…’ (Andersson & Simmons 2006)

The ‘direct phenotypic’ and ‘sensory bias’ mechanisms imply direct selection on the mate preference and the ‘runaway’ selection and ‘indicator’ mechanisms suggest indirect selection on the mate preference (Andersson and Simmons 2006). In the case of the ‘genetic compatibility’ mechanism, rather than favouring any particular trait, mate choice evolves because it conveys non-additive genetic benefits (Andersson & Simmons 2006). They thus saw a heritable component in mate preference as a necessary condition for intersexual selection to occur. This assumption is used in formal models such as those that seek to reconstruct ‘runaway’ selection (e.g. O’Donald 1980; Kirkpatrick 1982; Lande 1981) and the ‘handicap’ principle (Grafen

1990). It is also implicit in Buss's (1989) major cross-cultural study of mate preference where the methodology was based on the assumption that genes associated with mate preferences selected in ancestral populations would also be reflected in modern populations.

Empirical evidence of mate preference being subject to genetic influence is available. For example, paternal inheritance of mate preference in female moths (*Utetheisa ornatrix*) has been shown (Iyengar et al 2002) while experimental manipulation of female mate preference in stalk-eyed flies *(Cyrtodiopsis dalmani*)) has demonstrated genetic influence (Wilkinson & Reillo 1994). Evidence of female preference and male traits apparently evolving in parallel in the wild has also been found in guppies (*Poecilia retrailata*) (Houde & Endler 1990). Among humans, female mate preference for male odour has been traced to HLA (human leukocyte antigen) alleles which are inherited paternally (Jacob et al 2002) while a mate preference that leads to avoidance of spouses with HLA haplotypes that are the same as one's own has been demonstrated (Ober et al 1997).

The assumption being made in this study is therefore that if intersexual selection has acted on human altruism one would expect to find variation in mate preference towards altruistic traits to be subject to genetic influence. As the MPAT scale was developed to measure this mate preference (see Chapter 3) responses to this scale should, on this basis, be heritable. It is, however, not possible to rule out heritable variation in the expression of this mate preference being subject to random or pleiotropic genetic effects – rather than directional selection. This alternative explanation appears implausible since mate preferences are usually central to individual fitness and so genes associated with random or pleiotropic effects in the mate preference are likely to have been quickly driven to extinction as a result. But this assumption is the very one I am trying to test and so there is a risk of circularity here. Establishing whether mate preference towards altruistic traits is heritable therefore meets a necessary but not a sufficient condition for testing whether altruistic traits may be sexually selected

This test is made more exacting when one considers that, for intersexual selection to work, variation in the preferred trait (i.e. 'altruistic personality' as measured by the SRA scale (Rushton et al 1981)) must also be subject to genetic influence. The heritability of the preferred trait is less specifically indicative of sexual selection as demonstrating its heritability would presumably also be consistent with other proposed origins for altruism, such as indirect reciprocity or group selection or gene/culture co-evolution. Also, under some models (Heywood 1989; Hoelzer 1989) the heritability of the preferred trait is not required. Nevertheless if both mate preference towards altruistic traits and 'altruistic personality' were subject to heritable variation then this would be consistent with the proposed link between sexual selection and human altruism towards non-kin.

One final point about heritable variation needs to be made here. It may be possible for a trait to be under genetic influence (i.e. to be highly heritable) but not subject to variation if directional selection has removed all variation (i.e. what is suggested by the 'lek paradox' (Fisher 1958)). However, as discussed in Section 2.3.3, additive genetic variation in sexually selected traits in wild populations has been found to be actually greater than in other traits (Pomiankowski & Moller 1995; Gangestad & Simpson 2000; Amqvist & Rowe 2005). It is therefore a reasonable assumption that heritable variation in both mate preference and preferred trait will be displayed if they are associated with sexual selection.

6.1.4 Use of Twin Studies in Measuring Heritable Variation in a Trait

Given that heritable variation in mate preference towards altruistic traits and ‘altruistic personality’ is consistent with sexual selection acting on altruistic traits, the question then arises as to how this could be measured. One approach would be to use a twin study design to assess whether there is a heritable component in variation in responses to the MPAT and SRA scales.

It has been estimated that one in eighty-five births involve twins (Plomin et al 1997). Identical or monozygotic (MZ) twin births result from the further division of the zygote some time during the first 10-14 days after fertilisation. MZ births are not thought to be influenced by heredity or demographic factors (Kyvik 2000). Non-identical or dizygotic (DZ) twin births are the consequence of double ovulation, fertilisation and implantation and they are known to be related to heredity and maternal age (Kyvik 2000).

Twin study designs are based on the fact that MZ twin pairs share all their genes while DZ twin pairs have a 50% probability of sharing any given gene. Assuming that there is no overall difference between the family environments shared by MZ and DZ twins, it follows that any greater similarity in a particular trait between MZ twins must be due to genetic effects. It also follows that any difference among MZ twins can only be attributed to the effects of the environment. The basic objective of a twin design is thus to correlate scores between MZ twin and those between DZ twins and analyse any difference between the two in the light of this logic.

Twins studies have been used extensively since 1924 (Spector 2000) to investigate the effects of environment and heredity on diseases and medical conditions (e.g. Spector & MacGregor 2002), on abilities and personality characteristics (e.g. Loehlin & Nichols 1976) and on behavioural traits (e.g. Cherkas et al 2004). Many statistical methods employed in twin studies rely on the concept of likelihood introduced by Fisher and developed under the ‘maximum likelihood’ approach to estimation in human quantitative genetics (Jinks and Fulker 1970). Jinks and Fulker (1970) suggested that complex models for human variation could be simplified under the assumption of polygenic inheritance and that the goodness of fit of a model should be tested before judging the importance of the parameter estimates. Since that time various software packages have become available that allow statistical modelling of twin data (e.g. LISREL, Mx program).

6.1.5 Are Twin Studies a Sound Method for Estimating Heritability?

Twin studies have been the subject of much controversy over the years, not least because they claim to resolve the degree to which nature and nurture may influence variation in a particular trait. One aspect that has been particularly questioned is the assumption that there are no systematic differences in the ways MZ and DZ twins are brought up by parents and treated by each other (the equal environment assumption) (Rose et al 1984; Hopper 2000). There is, indeed, some evidence that MZ twins do tend to be treated differently to DZ twins (Loehlin & Nichols 1976). The question then arises as to how large an effect this has and whether it leads to over-estimation of genetic effects as critics of twin studies claim. An important insight into this question was offered by a study of twins where zygosity had been wrongly labelled. As a result, the effects of parents wrongly treating MZ twins as DZ twins and vice versa could be assessed (Scarr & Carter-Saltzman 1979). After correctly matching the twins, the researchers found that, as measured by intellectual and personality scales, the twins resembled each other according to their true zygosity and not by the way they were treated by parents and themselves. Thus where environmental dissimilarity was apparently present this did not appear to have exerted a major influence on the trait in question compared with the effects of actual zygosity.

In this debate it has also been pointed out that the effects of a common family environment (as opposed to the twin’s own unique environment) may dissipate as twins become adults and start to live separate lives (Plomin et al 1997; Hopper 2000). It may therefore be wise to assess the equal environment assumption in the light of the particular trait being examined (Hopper 2000). In the case of mate preference towards altruistic traits, the fact that subjects are adults is likely to reduce the importance of the common family environment on variation in responses. Also, if these mate preferences only developed during puberty then the effects of a shared family environment may be correspondingly reduced.

Another question is how generalisable the results obtained from twin studies are to the rest of the population. Might there not be important differences between twins and other people in aspects of behavioural traits? Although some differences have been found between twins and singletons at birth (e.g. twins tend to have a lower birth weight) and during childhood (Kyvik 2000; Johnson et al 2002) twins have not been found to be systematically different from singletons in terms of personality (Johnson et al 2002). It thus appears legitimate to draw inferences about mate preference towards altruistic traits in the wider population from a twin sample.

Given the logic outlined above, the objective of this study will therefore be to test the following prediction:

Prediction 3: That variation in mate preference towards altruistic traits, as measured by responses to the MPAT scale, and 'altruistic personality', as measured by responses to the SRA scale, will be subject to genetic influence.

6.2 Methods

6.2.1 Sample

The Twin Research and Genetic Epidemiology Unit based at St. Thomas's Hospital, London consists of nearly 10,000 adult twins aged between 18 and 80 from all over the UK. This volunteer sample was recruited by media campaigns and is predominantly female. Since its inception in 1993 the Unit has participated in many successful research projects into many common diseases previously thought to be predominantly environmental (Spector & MacGregor 2002).

Details of the ‘twin days’ organised by the Unit can be found in Chapter 4 (Section 4.2.1). In this study I was solely concerned with twin pairs and I obtained responses from a total of 178 twin pairs or *n* = 356 twins. The Unit provided details of the zygosity of each twin. Eighty were MZ twin pairs (female: *n* = 70; male: *n* = 10) and 97 were DZ twin pairs (female: *n* = 87; male: *n* = 10) with one twin pair of unknown zygosity. The age range of the sample was substantial (from 18 to 80 years) with a mean age of 55.9 years.

6.2.2 Procedure

The same questionnaire as that employed in Chapter 4 (Study 2) was used. A certain amount of duplication with that study in use of subjects was involved in that twins who reported that they were married or living with a long-term partner were also included in this study (*n* = 170). As in Chapter 4, subjects were blind to the prediction being tested. I observed the twins completing the questionnaire and found no evidence of collusion between them in how they responded to individual items. To help preserve the statistical power of the sample, where subjects failed to respond to individual items, the same process of mean substitution as that reported in Chapters 4 and 5 was employed.

6.2.3 Statistical Analysis

One method for estimating heritable variation proposed by Falconer & Mackay (1996, p. 171-174) was used to carry out initial estimation of whether heritable variation was present in this sample. This involved computing the mean correlations between MZ twins and between DZ twins, subtracting the mean DZ correlation from the mean MZ correlation and doubling the difference. This produces an estimate that is close to broad-sense heritability (i.e. the ratio of total genetic variation to total phenotypic variation) (Falconer & Mackay 1996).

This approach however offers only an approximate guide to the degree of heritable variation and does not separate additive and dominance genetic effects. A more sophisticated approach is available through use of Mx software (Neale & Cardon 1992, Neale 1997; http://www.vcu.edu/mx). Mx software was employed to perform genetic model fitting on the raw data with the assistance of the Social, Genetic and Developmental Psychiatry (SGDP) Centre at the Institute of Psychiatry, Kings College, London who have expertise in the use of this software. The components in variation in twin studies can be defined as follows:

- additive genetic effects (A);
- dominance genetic effects (D) (where interactions between alleles occur at the same locus. Dominance effects are indicated where the heterozygote does not fall mid-way between two homozygotes);
- common environmental effects particular to the twins' family (C);
- unique environmental effects (E) that are particular to the individual twin. This component also includes an estimate of measurement error.

It is however not possible to have more parameters than predicted statistics in the Mx program and thus only three parameters could be estimated. Parameter E has to be included as it contains the estimate for measurement error. Fortunately it is possible to initially establish the relative size of C and D, thus determining whether an ACE or ADE model should be fitted. C is considered to be large where the DZ correlation is greater than half the MZ correlation while D is considered to be large where the DZ correlation is less than half the MZ correlation. With the MPAT scale data, the DZ correlation was substantially less than half the MZ correlation (see Table 6.1) while in the case of the SRA scale data the DZ correlation was only slightly less than half the MZ correlation (see Table 6.2 below). An ADE model was therefore fitted in both cases.

The sample obtained showed a number of distinct characteristics. It was predominantly female and so, in view of the sex differences in gene expression found in some twin studies (Neale & Cardon 1992), an all-female sample was analysed firstly. Also, as the sample contained a substantial age range, an age regressed female-only sample was analysed to establish whether age effects might account for any differences between MZ and DZ twin pair responses. Finally, to provide a comprehensive analysis, an age and sex regressed sample of all subjects was produced. Thus three sets of analyses were carried out to determine whether one or a combination of these characteristics may have accounted for the results found.

The Mx software produces saturated and genetic models. The former allows comparison of the fit between the data and the model in terms of the equality of variances among and between the MZ and DZ twins and the means among and between the MZ and DZ twins. It thus offers a test of the overall soundness of the data indicated by a chi-squared statistic and its p-value. It is also allows computation of mean correlations between MZ and between DZ twin pairs, as discussed above and confidence intervals around these estimates.

The genetic model produces an estimate of the contributions of additive, dominance and unique environmental effects on the variation found and gives upper and lower 95% confidence intervals for each estimate. The output also tests the fit between data and genetic models as measured by chi-squared statistics. To assess the significance of individual parameters, each one is removed to produce various sub-models (i.e. DE, AE and E models). Where a parameter is dropped and the chi-squared statistic is significant this demonstrates that the parameter removed explains a significant proportion of the variance in the response variable. The overall effect of genotype (i.e. with additive and dominance genetic effects removed) on observed variation was tested by comparing the E sub-model with the ADE model.

6.3 Results

6.3.1 Estimated Heritability Based on Mean Correlations between MZ and DZ Twins: MPAT and SRA Scale Scores

An initial estimate of heritability based on the method proposed by Falconer and Mackay (1996) was carried out on responses to the MPAT and SRA scales using the Mx program. Taking the female-only sample as an example, this produced a very high estimate of heritable variation in response to the MPAT scale (see Table 6.1) but a more modest one in relation to the SRA scale (see Table 6.2).

Table 6.1. Heritability estimates of responses to the MPAT scale based on Falconer and Mackay (1996): female-only sample

	Correlation	Confidence Intervals (95% confidence)	
		Lower	Higher
MZ	0.591	0.414	0.725
DZ	0.095	-0.126	0.306
Estimated Heritability ((MZ – DZ)*2)	0.992		

Table 6.2. Heritability estimates of responses to the SRA scale based on Falconer and Mackay (1996): female-only sample

	Correlation	Confidence Intervals (95% confidence)	
		Lower	Higher
MZ	0.467	0.257	0.634
DZ	0.213	-0.0035	0.4098
Estimated Heritability ((MZ – DZ)*2)	0.507		

6.3.2 Heritability Estimates: MPAT Scale Scores

In relation to the MPAT scale data, the equality of means and variances between the MZ and DZ twin pairs and between total MZ and total DZ twin pairs were examined for all three sets of statistics (see Table 6.3). These were all found to be non-significant, with one exception, which indicated that the data generally provided a sound basis upon which to proceed.

Table 6.3. Equality of means and variances among and between MZ and DZ twin pairs (MPAT scale data)

	Means		Variances	
	χ^2	p	χ^2	p
Female-only				
MZ Twin Pairs	0.558	0.455	1.250	0.264
DZ Twin Pairs	0.328	0.567	0.418	0.518
MZ and DZ Twins	3.111	0.375	2.073	0.557
Female-only: Age Regressed				
MZ Twin Pairs	1.141	0.285	0.852	0.356
DZ Twin Pairs	0.325	0.568	0.669	0.413
MZ and DZ Twins	5.265	0.153	1.854	0.603
Total: Age and Sex-Regressed				
MZ Twin Pairs	1.038	0.308	3.876	0.049
DZ Twin Pairs	0.322	0.570	1.569	0.210
MZ and DZ Twins	5.546	0.136	6.159	0.104

The fit between the MPAT scale data and the various models is illustrated in Table 6.4. The standardised parameter estimates of the genetic models fitted for the MPAT data are detailed in Table 6.5.

Table 6.4. Fit between data and genetic models (MPAT scale data)

Model	FIT: *-2LL* (two times log-likelihood of data)	*df*	No. of Parameters	Difference χ^2	*df*	*p*
Female-only						
Saturated	1949.725	298	10	-	-	-
ADE	1955.178	304	4	-	-	-
DE	1955.178	305	3	0.000	1	1.000
AE	1958.590	305	3	3.412	1	0.065
E	1984.870	306	2	29.692	2	< 0.001
Female-only: Age Regressed						
Saturated	1940.562	298	10	-	-	-
ADE	1948.164	304	4	-	-	-
DE	1948.164	305	3	0.000	1	1.000
AE	1951.936	305	3	3.771	1	0.052
E	1977.639	306	2	29.474	2	< 0.001
Total: Age and Sex-Regressed						
Saturated	2198.789	338	10	-	-	-
ADE	2211.017	344	4	-	-	-
DE	2211.017	345	3	0.000	1	1.000
AE	2214.721	345	3	3.705	1	0.054
E	2239.749	346	2	28.733	2	< 0.001

Table 6.5. Standardised parameter estimates (± 95% confidence intervals) of the ADE genetic model fitted: responses to the MPAT scale

Sample	Additive Genetic	Dominance Genetic	Unique Environment
	(95% Lower and Upper Confidence Intervals)		
Female-only	0.00 (0 - 0.6128)	0.6044 (0 – 0.7228)	0.3956 (0.2772 – 0.5663)
Female-only: Age Regressed	0.00 (0 – 0.5769)	0.6004 (0 – 0.7198)	0.3996 (0.2802 – 0.5711)
Male and Female: Age and Sex Regressed	0.00 (0 – 0.5476)	0.5686 (0 – 0.6906)	0.4314 (0.3094 – 0.6009)

6.3.3 Heritability Estimates: SRA Scale Scores

With regard to responses to the SRA scale, the data were shown to provide a sound basis upon which to work with all chi-squared values being non-significant (see Table 6.6).

Table 6.6. Equality of means and variances among and between MZ and DZ twin pairs (SRA scale data)

	Means		Variances	
	χ^2	*p*	χ^2	*p*
Female-only				
MZ Twin Pairs	0.498	0.481	0.000	0.985
DZ Twin Pairs	0.091	0.763	0.608	0.436
MZ and DZ Twins	0.604	0.896	0.621	0.892
Female-only: Age Regressed				
MZ Twin Pairs	0.257	0.612	0.005	0.944
DZ Twin Pairs	0.352	0.553	0.380	0.538
MZ and DZ Twins	0.984	0.805	0.463	0.927
Total: Age and Sex-Regressed				
MZ Twin Pairs	0.060	0.807	0.811	0.368
DZ Twin Pairs	0.192	0.662	0.323	0.570
MZ and DZ Twins	0.298	0.960	1.138	0.768

The fit between the SRA scale data and the various models is illustrated in Table 6.7. The standardised parameter estimates of the genetic models fitted for the SRA data are detailed in Table 6.8.

Table 6.7. Fit between data and genetic models (SRA scale data)

Model	FIT: *-2LL* (two times log-likelihood of data)	*df*	No. of Parameters	Difference χ^2	*df*	*p*
Female-only						
Saturated	2280.060	289	10	-	-	-
ADE	2229.279	295	4	-	-	-
DE	2230.002	296	3	0.723	1	0.395
AE	2229.328	296	3	0.049	1	0.825
E	2249.023	297	2	19.743	2	< 0.001
Female-only: Age Regressed						
Saturated	2218.374	289	10	-	-	-
ADE	2219.839	295	4	-	-	-
DE	2220.308	296	3	0.470	1	0.493
AE	2219.943	296	3	0.140	1	0.747
E	2236.346	297	2	16.507	2	< 0.001
Total: Age and Sex-Regressed						
Saturated	2520.839	328	10	-	-	-
ADE	2522.274	334	4	-	-	-
DE	2522.701	335	3	0.426	1	0.514
AE	2522.378	335	3	0.104	1	0.747
E	2538.494	336	2	16.220	2	< 0.001

Table 6.8. Standardised parameter estimates (± 95% confidence intervals) of the ADE genetic model fitted: responses to the SRA scale

Sample	Additive Genetic	Dominance Genetic	Unique Environment
	(95% Lower and Upper Confidence Intervals)		
Female-only	0.370 (0-0.6108)	0.0986 (0-0.6155)	0.5313 (0.3781-0.7258)
Female-only: Age Regressed	0.2966 (0-0.5864)	0.1454 (0-0.6005)	0.5580 (0.3966-0.7636)
Male and Female: Age and Sex Regressed	0.2712 (0-0.5521)	0.1400 (0-0.5677)	0.5888 (0.4300-0.7838)

6.4 Discussion

The information contained in Tables 6.4 and 6.7 provides the key to testing whether genotype exerted a significant effect on variation in responses to the MPAT and SRA scales. With the environmental (E) sub-model both additive and dominance genetic effects have been removed. It can be seen from Table 6.4 that the effect of removing them is significant in the MPAT scale data, demonstrating that genotype is exerting a significant influence on variation in mate preference towards altruistic traits in all three sets of statistics. This finding is consistent with the strong genetic component suggested by Falconer and MacKay's method (1996). In the case of the SRA data, genotype also exerted a significant influence on 'altruistic personality' in all three sets of statistics.

It was not possible to separately measure additive and dominance genetic effects as the lower bounds of the confidence intervals were zero. Examination of the data suggests that dominance genetic effects may exert a greater influence in the MPAT scale data and additive genetic effects a larger effect in the SRA scale data. However, data from a bigger sample are required before these initial indications can be confirmed.

The key point, however, is that both mate preference and preferred trait, as measured by responses to the MPAT and SRA scales, have been found to be subject to significant genetic influence, thus confirming Prediction 3. These findings are thus consistent with sexual selection having acted on human altruism towards non-kin and therefore provide empirical support for the sexual selection hypothesis. Taken with evidence for mate choice on the basis of altruistic traits and stronger female mate preference towards altruistic traits, reported in Chapters 4 and 5, these three studies together provide persuasive evidence in favour of the sexual selection hypothesis to account for human altruism towards non-kin.

I am not aware of a twin study reported in the literature that specifically measures the heritable variation in a mate preference and preferred trait as a means of examining a link between sexual selection and the particular human trait involved. This is, therefore, believed to be the first time that such methodology has been employed to investigate the possible impact of sexual selection on a human trait.

As discussed in Chapter 2, Darwin (1871) was the first to propose that sexual selection may have exercised a powerful influence in human evolution of. More recently, Miller (2000) has suggested that distinctive human characteristics such as advanced cognitive ability and language may have evolved under sexual selection. The difficulty has always been in taking these generalised speculations, however plausible, and using them to generate hypotheses that can be tested. The methodology employed here could potentially enable hypotheses concerning the influence of sexual selection on other human traits to be generated and tested. Essential requirements are firstly the development and testing of reliable and valid psychometric scales to measure mate preference and preferred trait and secondly their use in a well-conducted twin study.

This methodology offers an advantage particularly in understanding the origins of human behavioural traits. The fossil record readily provides evidence of morphology but inferences about behaviour from the fossil record are far more difficult to make and are usually subject to alternative interpretations. Large-scale cross-cultural studies, like that conducted by Buss (1989), offer an approach to investigating the impact of evolutionary adaptation through identifying trends that are common to all cultures, but it is still possible to object that environmental factors could still have influenced all samples (e.g. Wallen 1989; Zohar & Gutmann 1989; Eagly & Wood 1999). The methodology used here offers not only a new approach to understanding the evolution of behavioural traits but also a test of the purely environmental interpretations of the results of Buss's study (1989).

Earlier, it was suggested that the stronger female mate preference towards altruistic traits reported in Chapter 5 might be explained by the 'social role theory of gender' (Eagly & Crowley 1986) or the 'structural powerlessness' models (e.g. Wallen 1989, Moore et al 2006). Evidence of both genetic and environmental effects acting on variation in mate preference towards altruistic traits presented here makes a purely environmental interpretation of this previous result difficult to sustain.

Estimating heritability in mate preference, as measured by a psychometric scale, does not, however, provide a sufficient test of the action of sexual selection since the heritability of the mate preference can be maintained by random or pleiotropic genetic effects, although this appears very unlikely – as discussed above. In contrast, the heritability of the preferred trait can be readily attributed to the effects of other selective processes (e.g. indirect reciprocity). However, the two taken together – genetic influence on mate preference and preferred trait – provides a valuable indication of whether sexual selection has influenced a particular human trait.

Evidence for mate choice on the basis of the trait in question would also meet another necessary condition, as would significant sex differences in mate preference where these are predicted by an evolutionary scenario. Thus the combined techniques of biology and evolutionary psychology provide a relatively simple methodology that could offer new insights into the role played by sexual selection in human evolution.

6.6 Summary

- Variation in both mate preference towards altruistic traits, as measured by the MPAT scale, and ‘altruistic personality’, as measured by the SRA scale, have been shown to be subject to significant genetic influence. This finding is consistent with human altruism towards non-kin having evolved as result of sexual selection.
- This evidence of genetic influence calls into question possible interpretations of the stronger female response to the MPAT scale discussed in Chapter 5 that rely solely on environmental factors.
- The methodology employed in this study could be used to investigate the possible role of sexual selection in the evolution of other human traits.

CHAPTER 7.VOLUNTARY ACTIVITY ON BEHALF OF OTHERS: THE INFLUENCE OF ALTRUISTIC AND OTHER MOTIVATIONS ON THIS BEHAVIOUR (STUDY 5)

7.1 Introduction

7.1.1. Altruistic and Other Components in the Motivation to Volunteer:

In Chapters 3 to 6 a possible ultimate cause of human altruism towards non-kin was investigated through measurement of mate preference towards altruistic traits. In this chapter a particular form of altruistic behaviour itself will be examined – voluntary activity, performed without monetary reward, for the benefit of another individual or group. Here, the emphasis will be on the motivational mechanisms that contribute to the performance of an ostensibly altruistic act.

Some argue that, as biology explores the selective forces that result in changes in gene frequencies, it should not be concerned with an animal's intentions or motivations but only its observable behaviour (Ridley & Dawkins 1981). Unlike other animals, however, humans can be asked what factors they think motivates them and so this can be seen as an observable aspect of their behaviour. Motivations influence performance of the altruistic act upon which selection works and so I see this as a legitimate subject for biological enquiry. By focussing on volunteer motivation it is hoped that this will enable a broader perspective to be obtained on human altruism towards non-kin in this thesis.

In the case of the sexual selection hypothesis it is being suggested that the ultimate cause of altruism towards non-relatives was that it evolved to enhance fitness through improved reproductive success in ancestral populations. But this hypothesis is very unlikely to occur to volunteers in the modern world as a likely motivation for volunteering. It is being proposed that genes associated with sexual selection acted on altruistic traits and reached a certain frequency in ancestral human populations (see Chapter 2). As a result, these genes are expressed in a modern social environment in which voluntary activity represents an acceptable outlet for such a predisposition. Here I was interested in the motivations that lead to the performance of an ostensibly altruistic act – volunteering to help others. This chapter will therefore say nothing about the ultimate evolutionary causes of altruistic behaviour but will instead concentrate on the mechanisms by which an example of altruistic behaviour is carried into practice.

Initial reflection on why individuals perform voluntary activity, other than for strictly altruistic reasons, suggests a number of likely motivations. For example, it may be seen as an enjoyable activity to carry out in its own right, it may be a means of avoiding boredom in one's personal life, it may give the volunteer valued contacts with other people and it may bestow a longer-lasting sense of importance and self-worth to the individual concerned (Clary & Snyder 1991; Clary et al 1992, Omoto & Snyder 1995; Clary et al 1998). The extent of voluntary activity performed may also be primarily constrained by the amount of free time that an individual has available. Thus numerous reasons for volunteering other than purely an altruistic desire to help others can be envisaged.

7.1.2 Why Do People Volunteer to Help Others?

The social psychology literature has sought to identify and measure the various components of volunteer motivation (Cnaan & Goldberg-Glen 1991). Studies, for example, by Frisch & Gerrard (1981) and Latting (1990) have used factor analysis to infer that both ‘altruistic’ and ‘egoistic’ motives were present in volunteer motivation while a study by Cnaan & Goldberg-Glen (1991) interpreted a single factor, although these authors recognised ‘altruistic’, ‘egoistic’, ‘social’ and other motives within that single factor. A study of the motivation of AIDS volunteers (Omoto & Snyder 1995) resulted in the extraction of five factors while another study of volunteering indicated a six-factor solution (Clary et al 1992; Clary et al 1998). In these last two studies sub-scales both referred to as ‘values’ were employed and can be seen as describing a purely altruistic component in volunteer motivation (i.e. a perceived desire to help others). Scales are therefore available that can measure the relative influence of altruistic as opposed to what other components in the motivation to volunteer.

Much of the social psychology literature has, in the past, sought to deny the existence of any purely altruistic motive (Unger 1991), instead viewing altruistic acts as a form of disguised selfishness (Clary & Snyder, 1991). As Clary and Snyder (1991) comment, the debate is often about whether ‘the motivations underlying a helpful act are ever truly altruistic….as opposed to egoistic’. In a review of the social psychology literature, Batson and Oleson (1991) identified three main explanations put forward for envisaging altruism as based on ultimately selfish or ‘egoistic’ motivations:

- the ‘aversive-arousal reduction’ explanation which sees the goal of the altruist being to reduce the empathic emotion experienced by the altruist towards a less fortunate individual. As this emotion is seen as aversive or unpleasant it is the motivation to reduce this emotion that results in altruistic behaviour;
- the ‘empathy-specific punishment’ which claims that we learn ‘through socialization that an additional obligation to help, and so additional guilt and shame for failure to help, are attendant on feeling empathy for someone in need.’;
- the ‘empathy-specific reward’ explanation which proposes that we learn through socialization that rewards follow in the form of praise, honour and pride from helping a person for whom we feel empathy.

Batson and Oleson (1991) then reviewed a series of studies where each of these explanations was tested empirically. For example, the ‘aversive-arousal reduction’ explanation was tested by giving subjects the opportunity to escape from a situation where altruistic behaviour was sought. Batson and Oleson (1991) concluded that there was little or no support for the three explanations typically put forward that ‘egoistic’ motivations account for apparently altruistic behaviour. The view was therefore taken that purely altruistic motivation is possible and that the dichotomy between altruistic and other components in volunteer motivation represents a valid and clear distinction.

7.1.3 Measurement of Volunteer Motivation

Voluntary activity requires time to decide whether to volunteer, followed by a search for an opportunity to do so and, typically, a sustained commitment of time and effort while the voluntary activity is carried out (Clary & Snyder 1991). It is thus an example of planned rather than spontaneous altruistic behaviour. Those who benefit from volunteer activity are unlikely to be related to the volunteer or ever be in a position to reciprocate the altruistic act at a later date (i.e. kin selection or direct reciprocity is unlikely to be an explanation). Performance of voluntary activity can, however, be seen as meeting the requirement of indirect reciprocity theory (Alexander 1979; Leimar & Hammerstein 2001) in that the reputation of the volunteer in relation to others (i.e. actual mates, potential mates, same sex allies and competitors) may be enhanced through this display of altruistic behaviour (e.g. Gintis et al 2001; Van Vugt 2007).

To measure volunteer motivation it was decided to employ the Volunteer Functions Inventory (VFI) (Clary et al 1998) in this study. The VFI is based on functional analysis, which can be defined as 'concerned with the reasons and purposes that underlie and generate psychological phenomena – the personal and social needs, plans, goals, and functions being served by people's beliefs and their actions' (Clary & Snyder 1991). Function in the sense it is used here emphasises immediate, proximate influences on motivation and should be distinguished from the concept of function typically understood by biologists (i.e. in terms of the selective forces acting on a trait during evolution). The motivational functions to volunteer identified in the VFI were:

- **values** (denotes the opportunities that volunteerism provides for individuals to express values related to altruistic and humanitarian concern for others);
- **understanding** (concerned with the new learning experiences offered by volunteering including the opportunity to use knowledge, skills and abilities that might otherwise go unpractised);
- **social** (about giving people the opportunity to be with friends and engage in activities viewed favourably by important others);
- **career** (denotes the career-related benefits through participation in volunteering);
- **protective** (identifies where volunteering protects the ego from negative aspects surrounding the self, including guilt and negative views of self);
- **enhancement** (centres on the ego's development and involves the positive strivings of the ego).

For each of the six motivational functions Clary et al (1992, 1998) developed a sub-scale of five items, resulting in 30 items for the VFI as a whole (see Table 7.1). Subjects are requested to rate the importance and accuracy of each item as a reason for volunteering on a scale from one to seven. The VFI was tested on various samples and its sub-scales were found to have satisfactory internal consistency and test/retest reliability while its predictive validity was supported by laboratory and field studies (Clary et al 1998). Responses to the VFI were not related to a measure of social desirability (Clary et al 1992), thus indicating that subjects had not been influenced by a desire to give a culturally acceptable response.

Table 7.1. Volunteer functions inventory (VFI): items related to each of the six motivational functions

(Item numbers denote order in which they are presented to subjects)

Values

2. I am concerned about those less fortunate than myself
8. I am genuinely concerned about the particular group I am serving
16. I feel compassion towards others in need
19. I feel it is important to help others
22. I can do something for a cause that is important to me

Understanding

12. I can learn more about the cause for which I am working
14. Volunteering allows me to gain a new perspective on things
18. Volunteering lets me learn things through direct, hands-on experience
25. I can learn how to deal with a variety of people
30. I can explore my own strengths

Social

1. My friends volunteer
3. People I'm close to want me to volunteer
6. People I know share an interest in community service
17. Others with whom I am close place a high value on community service
23. Volunteering is an important activity to the people I know best

Career

4. Volunteering can help me to get may foot in the door at a place where I would like to work
10. I can make new contacts that might help my career
15. Volunteering allows me to explore different career options
21. Volunteering will help me to succeed in my chosen profession
28. Volunteering experience will look good on my CV

Protective

7. No matter how bad I've been feeling, volunteering helps me to forget about it
9. By volunteering I feel less lonely
11. Doing volunteer work relieves me of some of the guilt over being more fortunate than others
20. Volunteering helps me work through my own personal problems
24. Volunteering is a good escape from my own troubles

Enhancement

5. Volunteering increases my self-esteem
13. Volunteering makes me feel important
26. Volunteering makes me feel needed
27. Volunteering makes me feel better about myself
29. Volunteering is a way to make new friends

7.1.4 'Altruistic Personality' and Volunteering

The Self-Report Altruism (SRA) scale (Rushton et al 1981) has been used widely as a measure of 'altruistic personality' elsewhere in this thesis. As discussed in Chapter 4, Rushton et al (1981) saw altruistic behaviour as a consistent personality trait rather than it being solely a specific response to a particular context, as others have often viewed it. Rushton et al's position was supported by their subsequent finding that responses to the SRA scale were influenced by broad-sense heritability (Rushton et al 1986). The reliability and validity of the SRA scale has been supported in various tests (Rushton et al 1981) (see also Chapter 4).

The concept of 'altruistic personality', as measured by the SRA scale, appears to correspond closely with what is described by the 'values' function of the VFI. Thus correlation between the two measures gives an opportunity to test whether they both assess a similar construct.

Use of the SRA scale in this study also enables comparison to be made with the responses of those in other studies in this thesis. Of particular interest is the question of whether volunteers in this study demonstrate a more developed 'altruistic personality' than the wider population. Such a comparison has considerable implications for understanding the relative importance of the altruistic component of volunteer motivation. For, if volunteers were found to have a more prominent 'altruistic personality' (as measured by the SRA scale) this would be consistent with an altruistic component playing a major role in the motivation to volunteer. If not, that would be consistent with the other motivational functions exercising a relatively more important role.

Two problems, however, suggested themselves in comparing the 'altruistic personality' of volunteers with others. Firstly, as discussed in previous chapters, a significant tendency was found for responses to the SRA scale to increase with age. This is not surprising in that older subjects will have had more opportunity to perform such acts than younger subjects, other things being equal. Age therefore had to be controlled for in the study design. Secondly, data from other studies used in this thesis contains subjects who themselves may have a more developed 'altruistic personality' than average. The twin sample comprised subjects who had volunteered to travel to a 'twin day' with only travel expenses as recompense while other subjects had taken the trouble to complete a questionnaire and return it by post. This will make it correspondingly more difficult to demonstrate a significantly higher response to the SRA scale in the volunteer sample.

7.1.5 Duration of Voluntary Activity as a Correlate of Volunteer Motivation

The VFI generates self-report data and these are often seen as open to biases, as discussed in Chapter 4 (e.g. Batson 1991; Feingold 1992). Subjects may be responding to a situation in ways they feel are appropriate to being a good volunteer (Allen & Rushton 1983) and responses may be *post hoc* justifications for voluntary work as opposed to reflecting the actual motivations that originally acted as springboards to carry out voluntary activity (Okun et al 1998, p. 620).

In the light of such potential bias it is important, as discussed in Chapter 4, to attempt to make an independent link between the self-report data and the actual behaviour they are supposed to measure (Zohar & Guttman 1989). One possible correlate of volunteer motivation is the length of time spent by volunteers actually performing voluntary activity (Unger 1991; Okun et al 1998; Omoto & Snyder 1995). If this index of volunteer commitment is correlated with responses to the sub-scales of the VFI the relative influence of each of the six motivational functions can be assessed – including, particularly, the relative impact of the ‘altruistic’ as opposed to the more ‘selfish’ components. Unfortunately reported duration of past voluntary activity itself generates self-report data and therefore both sets of responses, although completed in different forms, may be subject to the same systematic bias. This, therefore, cannot be seen as a fully satisfactory answer to the problem. The issue of using self-report data to measure human behaviour will be examined more fully in Chapter 8 (see Section 8.5).

7.1.6 Voluntary Activity and Sex

Females are thought to make up the majority of volunteers (Henderson 1983; Marrow-Howell & Miu 1989; Clary & Snyder 1991; Clary et al 1992; Ibrahim & Brannen 1997) and the possible reasons for this supposed pattern are of obvious relevance to this study. Of particular interest are any differences between females and males in responses to the six sub-scales, in reported duration of voluntary activity and the associations between these variables.

7.1.7 Overview of Study

The VFI will be used as a foundation of the study and, in particular, the relative effects of the ‘values’ as opposed to other motivational functions will be assessed. To this end, the SRA scale will be used to test whether it shares the same construct as the ‘values’ function of the VFI and whether volunteers display a higher than average ‘altruistic personality’ in contexts outside of voluntary activity. Evaluation of the relative importance of the altruistic as opposed to other components in volunteer motivation can thus be made. Correlation between reported duration of voluntary activity - seen as an index of volunteer commitment - and the six motivational functions of the VFI will also allow an insight into the relative effects of altruistic as opposed to other components in volunteer motivation.

7.2 Methods

7.2.1 The Volunteer Sample

A first step was to identify a suitable sample of volunteers willing to take part in the study. Fortunately, a potential sample of volunteers was available within the University of Nottingham itself. The Active Communities Initiative (ACI) was established in October 2002 to promote the University’s involvement in the wider community by encouraging employees and students to volunteer their time and effort to help others (First Steps: Active Communities Review 2004).

The ACI is managed by a Project Co-ordinator whose main role is to match the skills and time available of would-be volunteers with specific needs identified within the community. Examples of voluntary activity sponsored include participation in the Right to Read programme to promote greater literacy among schoolchildren, serving on boards of school governors, taking part in community arts activities, helping at an animal rescue centre, recycling old University computers for school and community use and redecorating community properties for public benefit. Focussing on volunteers co-ordinated by the ACI thus encompasses a variety of different forms of voluntary activity and goes some way to countering the criticism made of other studies that samples of volunteers are restricted to one site or program (Clary & Snyder 1991; Cnaan & Goldberg-Glen 1991; Okun et al 1998).

Volunteers willing to take part in the ACI had been identified following a survey of University employees and, as a result, a database of 357 actual and potential volunteers was available.

7.2.2. The Questionnaire

Permission was given by the Project Co-ordinator for the use of the ACI database in this study. A questionnaire (see Appendix 7.1) was constructed that included both the VFI and the SRA scale. Duration of voluntary activity was measured by asking volunteers to estimate the number of months over the previous five years when they had performed some form of voluntary activity. A period of over five years risked inaccuracy through poor recollection while a shorter period was seen as not being sufficiently representative. An open-ended question on what motivated subjects to perform voluntary activity that had not been suggested to them by the VFI was also added. Requests for basic demographic information such as sex, age, level of education and marital status were also made. To obtain an indication of how representative the sample was of the University workforce as a whole, questions were asked about employment category, pay rate and whether the subject worked full or part-time. The corresponding information for the population from which the sample was drawn was then obtained from the University's personnel department.

The questionnaire was tested on four volunteers at a pilot stage and a number of changes made in the wording as a result (e.g. 'résumé was replaced by the British equivalent 'CV'). To emphasise the original motivation and to avoid 'post hoc' justifications subjects responding to the VFI were asked to:

'rate how important or accurate each of these possible reasons for volunteering were for you when you originally decided to volunteer'

on a scale from one to seven.

7.2.3 Procedure

All of the 375 people on the ACI database (comprising 256 females, 115 males and 4 unknown) were contacted by e-mail during February 2005, informing them of the study and requesting that they complete the questionnaire.

A website was designed with the help of members of the School of Biology Information Technology team to enable subjects to respond anonymously on-line. The option of subjects printing off the blank questionnaire and returning a written version by internal mail was also given.

Nine days after the original e-mail was sent out a further e-mail was dispatched thanking those who had responded and reminding those who had not that it was not too late to respond. The website was closed some three weeks after the original e-mail was sent out.

7.2.4 The Sample

A total of 107 completed questionnaires were received - a response rate of 28.5 %. However, examination of responses to the question that asked over what period voluntary activity had been carried out over the previous five years revealed that 16 subjects had not carried out any voluntary activity in that period. These subjects may not have actually performed any voluntary activity in the past and their presence on the ACI database may have only indicated their willingness to do so in the future. These non-volunteers were therefore excluded from further analysis. This resulted in a sample of 91 subjects (62 female and 29 male) - a response rate of 24.3 %. The mean age of the sample was 39.4 years (± s.e. = 1.197).

7.2.5 Analysis of Data

Before correlations between the variables of interest were conducted the data were tested for normality of distribution using the one-sample Kolmogorov-Smirnov test. Those related to the VFI and SRA scales were found to be normally distributed while the count data related to reported duration of voluntary activity were not. Attempts to transform these data did not achieve a sufficient improvement and so non-parametric methods were employed there.

Principle components analysis was conducted on the data. The aim was to establish whether this sample exhibited the same characteristics as the samples observed by Clary et al (1998). A six-component solution, in line with the structure arrived at by Clary et al (1998) was specified using Varimax rotation with Kaiser normalization. Whether items grouped together under the same six components was examined, as was the resulting Scree plot.

In comparing the SRA scores of volunteers with those of the twin and spouse/partner samples analysis of covariance (ANCOVA) was employed with age fitted as a covariate. Cases where subjects were included in both the twin and spouse/partner sub-samples were removed. The standardised residuals were checked to see whether they were normally distributed.

Finally, comparison was made between the volunteer sample and the demographic characteristics of the population from which they were drawn – the University workforce. The three aspects where accurate information was available were sex, employment category and whether the subjects worked full or part-time. A small number of students in the volunteer sample were excluded for the purposes of this exercise.

7.3 Results

7.3.1 Characteristics of the Sample

The responses of subjects are detailed in Appendix 7.1, with the exception of those towards the VFI and SRA scales which are examined elsewhere. A total of 70 out of the 91 volunteers reported themselves as currently performing voluntary activity at the time when the survey was being carried out. Over the previous five years subjects reported performing some form of voluntary activity during a mean of 33.7 (± s.e. 2.52) months - that is, over more than half of the period.

Of those carrying out voluntary activity as a result of the Active Communities Initiative (ACI), subjects reported 58 separate forms of activity. By far the largest category involved working for or with children (35) and, of these, 17 mentioned the 'Right to Read' campaign. Subjects who had performed voluntary activity not associated with the ACI reported 52 separate forms of activity of which working with children also figured prominently (20).

7.3.2 Responses to VFI

Ratings of the importance and accuracy of each motivational function in terms of original reasons to volunteer, scored from one to seven, are outlined in Table 7.2 in ascending order. The internal consistency of each sub-scale, using Cronbach's alpha coefficient (α) (see Chapter 3), is also shown. Female volunteers allocated higher scores than males in response to five out of the six sub-scales (see Table 7.3), although only in relation to the 'understanding' sub-scale was a significantly higher score demonstrated.

Table 7.2. Volunteer functions inventory (VFI): mean scores, standard errors of mean (± s.e.) and internal consistency (Cronbach coefficient alpha (α)) of each sub-scale

Motivational Function (Sub-Scale)	Mean Score (± standard error of mean.)	Internal Consistency (coefficient α)
Values (altruistic concern for others)	5.38 (± 0.13)	0.79
Understanding (new learning experiences)	4.42 (± 0.15)	0.85
Enhancement (development of ego)	3.27 (± 0.14)	0.82
Career (career-related benefits)	2.46 (± 0.15)	0.89
Protective (protecting ego from negative aspects of self)	2.43 (± 0.12)	0.70
Social (being with friends, activities viewed favourably by important others)	2.10 (± 0.12)	0.78

Table 7.3. Female and male scores in response to volunteer functions inventory (VFI)

VFI Sub-Scales	Mean Scores (± standard error of mean)		Independent Samples t-test of Sex Difference
	Female	Male	
Values	27.23 (0.72)	26.14 (1.26)	$t_{89} = 0.80, p = 0.425$
Understanding	23.18 (0.83)	19.76 (1.55)	$t_{89} = 2.12, p = 0.037$
Social	10.48 (0.76)	10.55 (0.89)	$t_{89} = -0.05\ p = 0.958$
Career	13.15 (0.97)	10.45 (1.19)	$t_{89} = 1.65, p = 0.103$
Protective	12.90 (0.75)	10.59 (0.84)	$t_{89} = 1.87, p = 0.065$
Enhancement	16.37 (0.89)	16.28 (1.15)	$t_{89} = 0.06, p = 0.950$
Total VFI	103.31 (3.05)	93.76 (4.31)	$t_{89} = 1.79: p = 0.070$

7.3.3 VFI: Principle Components Analysis

The eigenvalues and total variance explained by each component is illustrated in Table 7.4.

Table 7.4. Principle components analysis: eigenvalues and total variance explained

Component	Eigenvalues	Total Variance Explained
1	7.31	24.37
2	3.67	12.24
3	2.98	9.94
4	2.13	7.11
5	1.50	4.93
6	1.30	4.34
7	1.19	3.97
8	1.02	3.40

Six components were specified and the loadings of the 30 items of the VFI on the components are shown in Table 7.5. In the case of five of the components, items loaded (with two exceptions) on the factors identified by Clary et al (1998). However, in the case of the ‘protective’ function the items were scattered among 4 factors with 3 of the 5 items showing heavy cross-loadings.

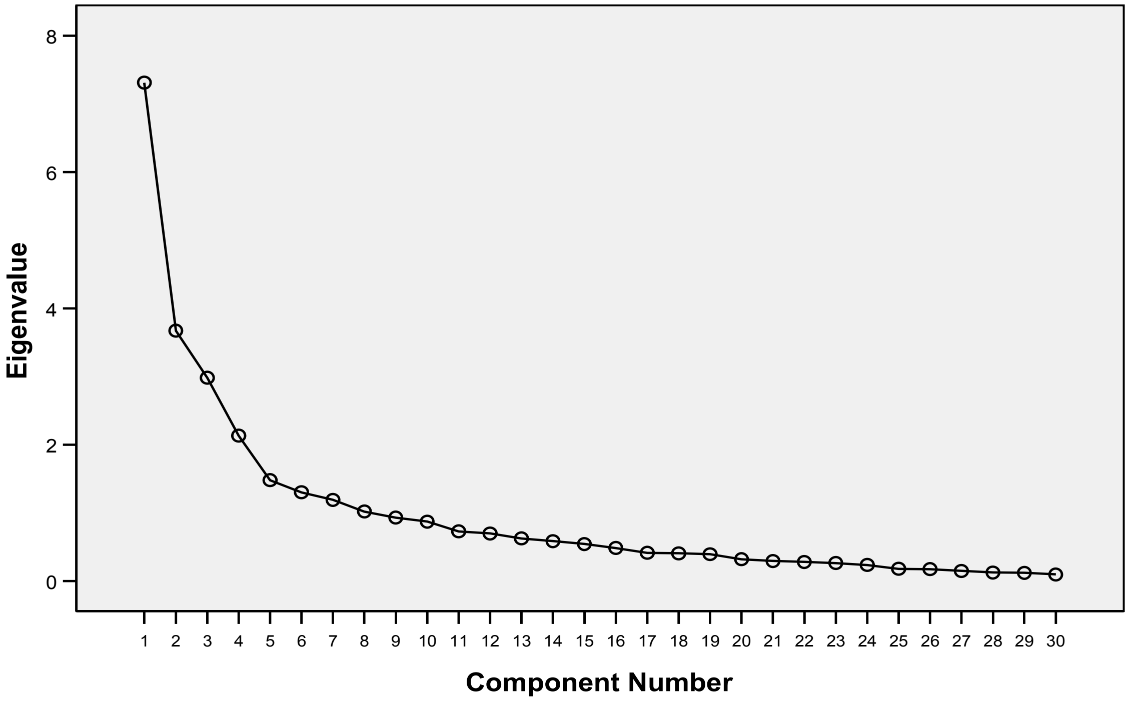
Table 7.5. Volunteer functions inventory (VFI): principle components analysis.

Rotated component matrix

VFI Sub-Scales with items	**Components (Loadings of Individual Items)**					
(see Table 7.1 for which items the numbers below represent)	1	2	3	4	5	6
Values						
2			0.72			
8			0.72			
16			0.76			
19			0.65			
22			0.70			
Understanding						
12	0.54					
14				0.58		
18				0.71		
25				0.74		
30				0.73		
Social						
1						0.51
3					0.64	
6					0.71	
17					0.82	
23					0.85	
Career						
4	0.79					
10	0.85					
15	0.84					
21	0.79					
28	0.65					
Protective						
7						0.78
9		0.51				
11				0.41		
20					0.41	
24						0.63
Enhancement						
5		0.59				
13		0.69				
26		0.82				
27		0.81				
29		0.50				

Examination of the resulting Scree plot, however, indicated a levelling off after the fourth component (see Figure 7.1). A four-component solution was therefore indicated.

Figure 7.1. Scree plot of principal components analysis of VFI Items



7.3.4 SRA Scale Responses

A significant positive correlation was found between the 'values' sub-scale of the VFI and the SRA scale scores ($r_{91} = 0.28$, $p = 0.008$), confirming the suggestion that they assess a similar construct. There was also a significant positive correlation between SRA scale scores and reported duration of voluntary activity over the previous five years ($r_s = 0.35$; $n = 91$; $p = 0.001$), a result consistent with 'altruistic personality' being associated with this index of volunteer commitment.

The mean SRA scale scores of the volunteer sample were similar to that of the combined sample of twins and their spouses and partners (see Table 7.6) although the mean age of the volunteer sample was markedly lower than that of the other sample. Controlling for the effect of age, the volunteer sample was found to have a significantly higher SRA score than that of the twin and spouse/partner sample (see Table 7.7).

Table 7.6 Mean SRA score of volunteer sample in relation to combined twin and spouse/partner samples

Sample	Mean Score (± standard error of mean)	Mean Age of Sample (± standard error of mean)	Sample Size
Volunteers	61.92 (± 1.14)	39.4 (± 1.20)	91
Twins, Spouses and Partners	61.15 (± 0.489)	52.56 (± 0.780)	332

Table 7.7. Analysis of covariance (ANCOVA) of responses to SRA scale of two samples (volunteer sample: *n* = 91 and combined sample: *n* = 332).

Term	*F (df)*	*P*
Age	2.541 (1,328)	0.112
Sample	4.433 (1,328)	0.036
Age*Sample	3.496 (1,328)	0.062

7.3.5 Results Involving Reported Duration of Voluntary Activity

Of the six VFI sub-scales, only one – the 'values' sub-scale – demonstrated a significant positive relationship with reported duration of voluntary activity over the previous five years (see Table 7.8). The 'careers' sub-scale showed a significant negative correlation.

Table 7.8. Correlations using Spearman Rank Correlation Coefficients between scores in response to the volunteer functions inventory (VFI) and its sub-scales and duration of reported voluntary activity (*n* = 91) (significant correlations in bold)

Motivational Functions (Sub-scales)	Months of voluntary activity over previous five years
Values	**$r_s = 0.225, p = 0.032$**
Understanding	$r_s = -0.124, p = 0.243$
Social	$r_s = 0.097, p = 0.363$
Career	**$r_s = -0.271, p = 0.009$**
Protective	$r_s = -0.050, p = 0.635$
Enhancement	$r_s = 0.003, p = 0.980$
Total VFI	$r_s = -0.070, p = 0.507$

Male volunteers reported a significantly longer duration of voluntary activity over the previous five years (Mann-Whitney: $z = 2.00, p = 0.045$).

7.3.6 Other Characteristics of Volunteer Sample

Females were over-represented in the volunteer sample compared with the University of Nottingham workforce (chi-squared test: $\chi_1^2 = 10.02$; $p < 0.01$) (see Table 7.9).

Table 7.9. Comparison of numbers in university workforce and volunteer sample by sex

	Numbers in Workforce (% age of total)	Expected Number in Sample	Observed Number in Sample (% age of total)
Female	3187 (51.8%)	43.5 (51.8%)	58 (69.0%)
Male	2967 (48.2%)	40.5 (48.2%)	26 (30.9%)
Total	6154	84	84

In terms of employment category the volunteer sample was untypical of the workforce from which they were drawn (chi-squared test: $\chi_5^2 = 58.16$: $p < 0.001$). The 'Administrative, Professional and Managerial' category was over–represented and the 'Manual' category under-represented in the volunteer sample (see Table 7.10).

Table 7.10. Comparison of numbers in university workforce and volunteer sample by employment category (students excluded)

Employment Category	Numbers in workforce	Expected Number in Sample	Observed Number in Sample
Academic	1164 (18.9%)	15.7 (18.9%)	19 (22.9%)
Administrative, Professional, Managerial	1709 (27.8%)	23 (27.8%)	50 (60.2%)
Manual	993 (16.1%)	13.4 (16.1%)	0 (0.0%)
Research	824 (13.4%)	11.1 (13.4%)	9 (10.8%)
Technical Services	541 (8.8%)	7.3 (8.8%)	4 (4.8%)
Other Employee	919 (14.9%)	12.4 (14.9%)	1 (1.2%)
Total	6154	83 *	83 *

* 1 subject did not record employment category

Part-time employees (defined as those contracted to work less than 30 hours per week) were under-represented in the volunteer sample (chi-squared test: $\chi_1^2 = 12.56$; $p < 0.001$) (see Table 7.11).

Table 7.11. Comparison of numbers in university workforce and volunteer sample according to full-time and part-time status (students excluded)

Hours Worked	Numbers in Workforce	Expected Numbers in Sample	Observed Numbers in Sample
Full-Time	4426 (71.9%)	60.4 (71.9%)	75 (89.3%)
Part-Time	1728 (28.1%)	23.6 (28.1%)	9 (10.7%)
Total	6154	84	84

7.3.7 Other Reasons for Volunteering

There were 41 responses to the request for other reasons for volunteering not covered by the VFI (see question 8: Appendix 7.1). Putting aside reasons for volunteering that closely mirrored the six motivational functions, the remaining 21 responses were examined to see whether any discrete ‘motivations of generic relevance to volunteerism’ (Clary et al 1998) might emerge (see Appendix 7.1). Nine responses were seen as inter-connected in that all mentioned a sense of fairness, equality, reciprocation and ‘giving something back’ as a motivational function served by volunteering.

7.4 Discussion

The demographic characteristics of the sample on which this study is based reflected some of the trends found in other volunteer studies (e.g. Unger 1991; Clary et 1992, Ibrahim & Brannen 1997, Clary et al 1998). Females comprised a disproportionately high percentage of the sample while both the administrative, professional and managerial and the full-time employment categories were over–represented in relation to the sub-population from which the sample was drawn (i.e. the University of Nottingham workforce).

Responses to the VFI in this sample followed a pattern similar in most but not all respects to that of other studies. The ranking of each sub-scale corresponded precisely with that found in two studies carried out by Clary et al (1998) in developing the VFI. One of these studies contained subjects of a similar mean age (40.9 compared with 39.4 years in this sample) while the other had a much younger mean age (21.25 years). Other studies where the VFI has been employed contained substantially older subjects (Clary et al 1998, Okun et al 1998) but showed similar although not identical rankings of the sub-scales to this sample.

When subjected to principal components analysis most items loaded together on to the components identified by Clary et al (1998). The main exception was the 'protective' function (i.e. identifies where volunteering protects the ego from negative aspects surrounding the self, including guilt and negative views of self) where items were scattered between other components. Thus subjects in this sample apparently failed to clearly recognise the 'protective' function as a discrete motivation to volunteer. However, Clary et al (1998) made it clear that contrasting samples might recognise motivational functions differently and so this may well have been a particular characteristic of this sample.

The design of this study has enabled new perspectives to be obtained on the motivation to volunteer, which has resulted in some interesting data. But before discussing these it is important to make the point that the sample on which the study is based is small (*n* = 91) relative to that of other volunteer studies (e.g. Clary et al 1998). The sample is also somewhat smaller than the figure of 100 deemed sufficient for factor analysis (Kline 1998, p. 73) and so all conclusions must be considered in this light of this reservation.

A principal aim of this study was to compare the ‘altruistic’ component in volunteer motivation with the five other motivations that resulted in the performance of an ostensible altruistic behaviour. The contrast between the ‘values’ sub-scale and the other five sub-scales of the VFI provided a basis for measuring this dichotomy. In this sample, as in other samples (Clary et al 1998), the ‘values’ sub-scale elicited the most positive response in terms of importance and accuracy as a reason for volunteering.

A correlate of volunteer motivation - reported duration of voluntary activity over the previous five years - was incorporated into the study design with the aim of measuring the relationship between responses to the six motivational functions and this measure of volunteer commitment. The significant positive relationship found with the ‘values’ motivational function gave support to it as a ‘predictor’ of volunteer commitment while, in contrast, the other five motivational functions demonstrated no such relationship. If the self-report measure of duration of voluntary activity was inaccurate because it had led to the systematic bias of exaggeration in response then this would have been reflected in non-significant correlations with all six motivational functions, which was not the case. Thus the importance of an altruistic component in volunteer motivation was reinforced and some doubt cast on the other five motivations as ‘predictors’ of volunteer commitment.

Another interpretation of this result is, however, possible. It may be that the five-year timescale, as an index of volunteer commitment, was too long to reflect the full range of motivations that prompted subjects to originally volunteer. The effects of the other five motivational functions might have been sustained over much shorter timescales than the five-year period of volunteer commitment. For example, in the case of the ‘understanding’ function, once new skills and experiences have been acquired or practiced, they may cease to possess their original power as a motivation. Once a career has been benefited, further voluntary activity may not lead to additional individual advantage and so cease to influence volunteer commitment. In the case of the ‘protective’ function, once a period of voluntary activity has been completed negative feelings about the ego may dissipate. In the case of the ‘enhancement’ function, concern with the ego’s development may be satisfied following a successful experience of volunteering. In the case of the ‘social’ function, the desire to make new friends may become less important as this objective was achieved or found elsewhere. Thus these functions may not be able to successfully predict volunteer commitment over a five-year period but may be accurate for the shorter timescales over which these motivational functions are satisfied.

In contrast, the ‘values’ function may be correlated with a continuing desire to volunteer that does not become satiated with prolonged exposure to volunteer activity. On this basis, the ‘values’ function may provide a more accurate predictor of long-term (e.g. five year) voluntary activity although not necessarily exercising a greater influence on the initial tendency to volunteer. One way of investigating this interpretation would be to carry out a longitudinal study using the VFI. Volunteers could be located at or about the time when they decide to become volunteers and the various scores of the VFI sub-scales correlated with the subsequent actual duration of voluntary activity. The VFI could then be re-administered to subjects over time to measure any trends in the importance given to each motivational function.

The relationship between duration of volunteer service found here and an altruistic component in volunteer motivation was, however, not reflected in another similar study. Okun et al (1998) also employed the VFI and correlated responses to it with a measure of ‘frequency of volunteering’, which did not correlate significantly with the ‘values’ motivational function but did with certain other motivational functions and the total VFI score. . Further research is thus required to investigate whether the patterns found in Study 5 can be replicated elsewhere.

The SRA scale is a valid and well-established measure of ‘altruistic personality’ (Rushton et al 1981; Rushton et al 1986) and the significant positive correlation found between it and the ‘values’ sub-scale confirmed that both measured a similar construct. The moderately strong significant correlation between the SRA scale responses and reported duration of voluntary activity confirmed a significant three-way relationship. This relationship, especially in the absence of any significant positive association between the other VFI sub-scales and reported duration of voluntary activity, gives additional support to the ‘values’ motivational function as a valid measure of an altruistic component in volunteer motivation and the principle source of sustained motivation among volunteers.

Given the assumption that there is an ‘altruistic personality’ consistently expressed in different contexts (see Section 7.1.5), a simple account of what motivates volunteers is that they exhibit this trait more prominently than the rest of the population. The comparison made between the volunteer and other sample was therefore instructive. The ANCOVA revealed a significant effect of ‘sample’ on SRA scale response (i.e. volunteers had a significantly more developed ‘altruistic personality’ after including age as a covariate). More research is, however, needed to investigate this comparison, comprising a random sample against which to compare the ‘altruistic personality’ of a sufficiently sized sample of volunteers.

The results reported here suggest a single altruistic component is present in volunteer motivation, a conclusion at odds with the various models in the social psychology literature discussed in Section 7.1.2. The other five motivational functions appeared perfectly logical motivations to perform this altruistic behaviour but did not significantly ‘predict’ long-term commitment to volunteering in this study. In responding to the VFI subjects may well have been making *post hoc* justifications of their motivation to volunteer rather than accurately expressing their original motivation. Further research is needed to investigate whether these results can be replicated, particularly in larger samples than were possible in this study and using actual rather than self-reported duration of voluntary activity. Further light can then be shed on the intriguing questions raised by this study.

7.6 Summary

- A significant relationship was found between responses to the ‘values’ sub-scale of the VFI and the SRA scale, suggesting that both measure a similar construct.
- A significant association between responses to both these scales and a measure of volunteer commitment was found.
- No significant relationship between the other five motivational functions of the VFI and this measure of volunteer commitment was found.
- Volunteers in this sample exhibited a significantly more developed ‘altruistic personality’, as measured by the SRA scale, than in another sample.
- These results are consistent with a single altruistic component being present in the motivation to perform voluntary activity. More research is required to investigate these findings further.

CHAPTER 8. GENERAL DISCUSSION

8.1 The Sexual Selection Hypothesis

Thirty years ago Zahavi (1977) proposed that altruistic behaviour towards non-kin evolved because it was a 'handicap' that accurately revealed an individual's condition and viability to others. It was an original and perceptive insight. However, while Zahavi's 'handicap principle', as a general mechanism to explain how sexual selection works, has become widely accepted (Andersson & Simmons 2006), a specific link between altruism and sexual selection has remained relatively under-explored. This may be because Zahavi emphasised the wider implications of 'costly signalling' including its effects on 'social prestige' between individuals rather than concentrating solely on sexual selection. Models that have explored Zahavi's concept of 'costly signalling' (e.g. Gintis et al 2001) have examined its effects on same sex coalition partners or competitors as well as mates, and have thus not focused exclusively on sexual selection.

The notion that altruism towards non-kin is a sexually selected behavioural trait has an elegant simplicity. Other accounts of how altruism evolved that rely, for example, on indirect reciprocity, reputation formation or 'competitive altruism' invoke a special set of processes to explain the phenomenon. These, in turn, require solutions to another set of problems peculiar to these processes (e.g. 'cheating', 'punishment', 'second-order cheating'). In contrast, under the sexual selection hypothesis, altruism is seen as a trait favoured by a widely recognised process (i.e. sexual selection) (Darwin 1871; Andersson & Simmons 2006). On grounds of the principle of parsimony alone this hypothesis therefore merits serious consideration. Yet there has been a strange reluctance to explore a link between sexual selection and altruistic traits in detail over the past thirty years.

In this thesis I have considered a link between altruism and all sexual selection mechanisms including Zahavi's 'handicap principle'. I have also suggested that the special circumstances of human evolution may have provided an additional boost in favour of the evolution of altruism towards non-kin. On this basis, I tested three predictions and found support for each one. I found evidence of mate choice on the basis of altruistic traits in one sub-sample although only suggestive evidence of it in the other. I found evidence of significantly stronger female mate preference towards altruistic traits in a sample of sufficient statistical power. Finally, I found evidence that both mate preference and preferred trait were subject to significant genetic influence. These three findings thus provide persuasive evidence consistent with human altruism towards non-kin having evolved as a result of sexual selection.

8.2 Implications for Understanding the Origins of Other Human Traits

The link between human sexual selection and altruism towards non-kin explored here has wider implications for understanding other aspects of human evolution. If the puzzle of human altruism can be resolved by it being seen as a sexually selected trait this leaves open the possibility that other puzzling human traits, such as language and advanced cognitive ability, might also have evolved on this basis. The results presented in this thesis therefore give support to the proposal made by Darwin (1871) and Miller (2000) that humans have been strongly influenced by sexual selection.

More attention thus needs to be given to a possible link between sexual selection and other human traits.

8.3 Implications for Non-Human Species

This thesis has concentrated on human altruism towards non-kin. The scenario presented here as to how altruism may have evolved certainly sees conditions particular to human evolution as promoting the process and it may indeed be that human altruism is a unique trait (Fehr & Fischbacher 2003). Perhaps altruistic behaviour in non-human species will eventually come to be seen as explained entirely by kin selection or mutualism, with no genuine examples of altruism towards non-kin being found. Research is, however, required to explore this question further. A good starting point would be the study of a link between altruism and the 'handicap principle' in Arabian Babblers (*Turdoides squamiceps*) (Carlisle & Zahavi 1986), as discussed in Chapter 2. The apparent reproductive benefit gained by male guppies that carry out predator inspection on behalf of their group (Godin & Dugatkin 1996) - thus apparently displaying altruistic towards non-kin – is another promising example.

8.4 Does the Sexual Selection Hypothesis Provide an Adaptive Explanation for 'Strong Reciprocity'?

'Strong reciprocity' is defined as altruistic behaviour (e.g. repaying gifts, punishing violation of cooperation) that persists in anonymous, one-off encounters with genetically unrelated strangers (Fehr & Henrich 2003). Evidence for this behaviour is available in the human cooperation experiments carried out by Fehr and Gachter (2002), as discussed in Chapter 1. ‘Strong reciprocity’ represents a serious problem for models that rely on direct reciprocity (Trivers 1971), reputation formation (Nowak & Sigmund 1998; Leimar & Hammerstein 2001), ‘competitive altruism’ (Roberts 1998) or a ‘raise the stakes’ relationship (Roberts & Sherratt 1998) as these appear to require the prompt of interactions with another individual or individuals to result in the expression of altruistic behaviour. The persistence of altruistic behaviour in one-off, anonymous encounters is explained under this theory by it being a maladaptation or ‘misfiring’ of a reciprocal process in a novel, modern environment to which evolution has not yet adjusted (Johnson et al 2003 though see Fehr & Gachter 2003). The key point is that indirect reciprocity theory is seen as only able to account for ‘strong reciprocity’ as a maladaptation (Fehr & Henrich 2003). It has been argued that altruism must be seen as an adaptive trait and that ‘alternative evolutionary approaches are needed to provide ultimate accounts of strong reciprocity’ (Fehr & Henrich 2003) that are adaptive.

The sexual selection hypothesis, as outlined here, proposes that increasing parental investment allied to the development of language, advanced intelligence and ‘sexual gossip’ (Miller & Todd 1998) could have extended reproductive competition on the basis of altruistic traits to all contexts (see Chapter 2). Thus genes favoured by sexual selection acting on altruistic traits might also be consistent with expression of such traits in one-off, anonymous encounters with genetically unrelated strangers. It is, for example, possible to imagine the altruists themselves subsequently giving an account of their behaviour in such encounters and being believed or not as a result of ‘sexual gossip’ by reference to their other altruistic behaviour. Thus a reproductive premium arising out of altruistic behaviour in these encounters would have been possible, thereby accounting for ‘strong reciprocity’ adaptively through the sexual selection hypothesis. The reader might also note that language and advanced intelligence could also account for indirect reciprocity being adaptive in anonymous, one-off encounters on a similar basis (i.e. as a result of ‘gossip’ among early humans). This point requires further debate elsewhere.

8.5 Objections to the Sexual Selection Hypothesis: Use of Self-Report Data

One objection to the evidence presented in these studies is that it is dependent on psychometric scales and self-report data. How subjects report that they would behave may be completely different to how they actually behave in practice. As discussed in earlier chapters, self-report data have been criticised on the grounds that they are open to biases (Feingold 1992) and should therefore not be taken at face value (Batson 1991). It has been suggested that self-report data are bound to be a reflection of social norms that affect male and female responses in contrasting ways (Zohar & Guttman 1989) and some have even argued that self-report data cannot be treated as trustworthy at all (Sudman & Bradbury 1982; Boyd & Richerson 1985).

A number of points can be made in response to these criticisms. Error caused by self-report data may be related to two causes – random error or ‘noise’ and systematic bias, possibly of unknown origin. If the self-report data were producing random responses then this would have been reflected equally in both the MZ and DZ twin samples employed in the twin study. The pronounced patterns of different mean correlations between MZ and DZ twin pairs contradict this concern. Likewise, when the MPAT and SRA scales were completed by different subjects (i.e. twins and their spouses/partners in Chapter 4), results from these two self-report scales were found to correlate significantly in the way predicted in one sub-sample. However much ‘noise’ there is present in the data, a signal was therefore detectable.

The charge of systematic bias in psychometric scales can be answered, in part, by testing the validity of the scale in question. Corroborative evidence that self-report data do actually reflect what they are supposed to measure is required (Russell & Bartrip 1989) and was sought here. Actual mate choice was examined to see whether degree of mate preference ‘predicted’ degree of ‘altruistic personality’ in the mate chosen and this was supported in one sub-sample. The validity of the SRA scale has been tested and effort made to test the validity of the MPAT scale in these studies. Its construct validity was confirmed in two contrasting samples and this process needs to be continued with further use of the MPAT scale. Another way in which systematic bias may have crept in was through gender bias being present in the MPAT scale itself. As discussed in Section 3.3.4, individual items might possibly suggest different sex roles (although these may tend to be reduced in contemporary culture) but an overall balance between ‘caring’ and ‘heroic’ (Eagly & Crowley 1986) sex roles was seen as maintained within the scale.

Despite the measures taken to account for systematic bias, all measurement of behaviour presents problems of some kind for the researcher. Alternative approaches such as using controlled experiments devised by the experimenter or direct observation of naturally occurring behaviour also present difficulties (Goldberg

1995). The solution employed in this thesis of using self-report data offers what was seen as a reasonable balance between accuracy and practicality.

8.6. Objections to the Sexual Selection Hypothesis: Lack of Measurement of Fitness Benefits and Costs

Another objection that could be raised is that no attempt was made in this thesis to measure the fitness benefits or costs of altruistic behaviour. In practice, it is extremely difficult to measure the effects of particular behavioural acts on the fitness of individuals, especially in long-lived species (Boyd & Silk 1997, p. 254), and so attempting this here was not seen as a sensible investment of time and effort. This difficulty is unfortunate as a key assumption in this thesis is that mate choice is likely to have a far more direct and powerful effect on individual fitness than ‘costly signalling’ to same sex others related to coalition formation (see Section 2.6.1). On this basis, sexual selection is seen as a far more likely origin for human altruism towards non-kin.

The inference drawn linking the behaviour of successful hunters in modern hunter/gatherer societies and their apparently fitness–enhancing altruism nevertheless makes a contribution to this question. Food sharing would have offered a prominent opportunity for altruism towards non-kin in early hominid societies and the evidence discussed in Chapter 2 (e.g. Kaplan & Hill (1985; Hawkes 1993) is promising. This inference requires consideration by anthropologists who may wish to challenge it and/or carry out further research to test whether it may be valid. Matching evidence of the fitness benefits under coalition formation could also be sought.

8.7 Further Research Required

The work carried out in this thesis has suggested an abundance of further research that could be conducted and which has already been discussed here and in previous chapters. Formal modelling of the scenario discussed in Chapters 2 and 5 in relation to how parental investment might have affected the sex roles of males and females and the possibility of mutual sexual selection in human evolution would be particularly valuable. It would help to throw light on the question of why no significant sex differences in the preferred trait (as measured by the SRA scale) could be found in any of the studies. These are substantial issues and until they are resolved we need to be cautious in placing too much reliance on the sexual selection hypothesis. A larger twin study would also be illuminating and enable accurate measurement of dominance and additive genetic effects on MPAT and SRA scale responses to take place. The methodology reported in Chapter 6 may help to identify other human behaviours that have been subject to the effects of sexual selection.

The most important need, however, is for a fundamental change in the way altruism towards non-kin is viewed by researchers in this field. For at least three decades a major effort has gone into theoretical modelling of direct and indirect reciprocity theory which has not produced a clear breakthrough in empirical evidence to support it (Hammerstein 2002; Stephens et al 2002; Fehr & Fischbacher 2003). Yet, over the past three decades, comparatively little attention has been given to a specific link between sexual selection and altruism towards non-kin. The sexual selection hypothesis may therefore represent the future for research into the great evolutionary puzzle of altruism towards non-kin.

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APPENDICES

APPENDIX 3.1

QUESTIONNAIRE

Rate the following statements according to what you think is desirable or undesirable in someone with whom you would like to have a relationship (ie a future husband, wife, boyfriend, girlfriend). Please take your time and think carefully before placing a tick in one of the boxes.

	Very Un-desirable	Quite Un-desirable	Neither Desirable nor Un-desirable	Quite Desirable	Very Desirable
Is generous towards other people					
Is willing to stand by friends 'through thick and thin'					
Spent a year helping children in an African orphanage					
Not bothered about being thought stingy towards other people					
Once defused a violent argument between two friends					
Occasionally willing to be dishonest if it pays					
Cares about the welfare of animals					
Preferred not to become involved when a friend was in danger					
Ran the London Marathon to raise money for a good cause					
Is always willing to give money to charity					
Once dived into a river to save someone from drowning					

Refused to help a friend in need					
Took part in a sponsored parachute jump to raise money for a charity					
Usually leaves a large tip in an expensive restaurant					
Is a ‘giver’ rather than a ‘taker’					
Got out of helping at a children’s Christmas party					
Regularly helps an elderly neighbour					
Donates blood regularly					
Not particularly bothered about other people					
Willing to ‘do the right thing’ even if it is risky to do so					
Tipped off the police about a local drugs dealer					
Volunteered to help out in a local hospital					
No longer acknowledges a friend who ‘has gone down in the world’ socially					
Has a caring attitude towards other people					
Usually tries to get out of paying for a round of drinks					

Is willing to rescue someone in danger					
Always willing to help other people's children					
Had information about a terrorist attack but kept quiet for fear of retaliation					
Once cared for a stray dog injured by a car					
Is a member of a Lifeboat Crew					
Helped clear people away from a suspect package found in an airport					
Ended a friendship with someone who was wrongly accused of a serious crime					
Unwilling to take a risk to help people in an emergency					
Once spent a weekend helping to repair a community hall without pay					
Thinks we'd all be better off if everybody looked after themselves					
Once intervened to protect someone being robbed by a youth					
Did not mind being thought a coward by refusing to help other people					
Got out of visiting a friend in a hospice					
Climbed a tree to rescue a neighbour's cat					

Volunteered to help without pay on a week’s holiday for disabled people					
Once got someone out of a crashed car before it burst into flames					
Tends to be selfish towards other people					
Once refused to give money to help starving people in Ethiopia					
Took some rubbish abandoned in the street to a local tip					
Once gave a quarter of annual income to help a friend in dire financial trouble					
Brave if called upon to rescue others					
Had a pet put down rather than pay the vet’s bill for an operation					
Once picked up a wallet dropped in the street and handed it into the police					
Is a member of a mountain rescue team					
Once stood by and let someone else rescue children trapped in a burning house					
Gives time freely to help others out					

APPENDIX 3.2

Please complete the following details about yourself by circling the correct answer:

1. Gender: Male / Female

2. Age: _______________

3. Marital Status:
Single
Married
Divorced
Living with Partner
Separated
Widowed

4. If you have not circled 'Married' are you currently in a close relationship?

Yes / No

5. Would you describe yourself as heterosexual:

Yes / No

6. Are you a United Kingdom national?

Yes / No

7. To which ethnic group would you describe yourself as belonging:

White European
African
Afro-Caribbean
Bangladeshi
Indian
Pakistani
Other Asian
Other

8. In terms of religion would you describe yourself as:

Anglican
Catholic
Other Christian
Agnostic/Atheist
Buddhist
Hindu
Islam
Jewish
Sikh
Other

Consent Form

Information from this questionnaire will be used by a researcher at the University of Nottingham who is investigating aspects of human behaviour.

Participation is voluntary. If you decide to take part all the information given by you will remain confidential and anonymous, and be used for the purposes of the research only. This consent form will be kept separate from the questionnaire in order to ensure anonymity.

If you are happy to take part then please complete the details below. Thank you for your cooperation.

Surname ____

First Name/s ____

Signed ___________________________

Date _______________

APPENDIX 3.4

MATE PREFERENCE QUESTIONNAIRE

Below is a random list of characteristics you may look for in a potential partner. Please rate each one according to how important they are to you. Take your time and think carefully before placing a tick in one of the boxes for each characteristic.

	Very Unimportant	Quite Unimportant	Quite Important	Very Important
Similar education				
Ambition and industrious				
Dependable character				
Refinement, Neatness				
Caring towards others				
Good health				
Good financial prospect				
Similar religious background				
Favourable social status or rating				
Sense of Fairness				
Good looks				
Sociability				
Desire for home and children				
Chastity (no previous experience in sexual intercourse)				
Generous towards others				
Education and intelligence				
Emotional stability and maturity				
Similar political background				
Pleasing disposition				
Willing to rescue others in an emergency				
Good cook and housekeeper				
Mutual attraction - love				

APPENDIX 3.5

QUESTIONNAIRE

Please enter your Smartcard number below. Alternatively, if you do not have your Smartcard available enter your date of birth. This will preserve your anonymity and is essential for the design of this experiment.

Smartcard No. --

Gender: Female / Male
(please circle)

Age: ------------------

Thank you for your help.

QUESTIONNAIRE: RETEST

Please enter your Smartcard number or your Date of Birth below – dependent on whichever you used when you completed the first part of this experiment. This will enable your response today to be linked with your previous response while preserving your anonymity.

Smartcard No. --
(or Birth Date)

Thanks again for your help

MATE PREFERENCES

Below are a list of characteristics and examples of behaviour that you may look for in a husband, wife or partner. Please rate each one according to how undesirable through to how desirable you think they are on the five-point scale below. Take your time and think carefully before placing a tick opposite each of the items.

Items	Undesirable → Desirable				
Has a dependable character					
Is ambitious and industrious					
Occasionally willing to be dishonest if it pays					
Ran the London Marathon to raise money for a good cause					
Is good looking					
Not bothered about being thought stingy towards other people					
Has a similar education to me					
Once dived into a river to save someone from drowning					
Got out of visiting a friend in a hospice					
Enjoys good health					
Donates blood regularly					
Shows refinement and neatness					
Regularly helps an elderly neighbour					
Has good financial prospects					
Once stood by and let someone else rescue children trapped in a burning house					
Has a similar religious background to me					
Volunteered to help without pay on a week's holiday for people with disabilities					

Item	Undesirable		→		Desirable
Has a favourable social status or rating					
Thinks we'd all be better off if everybody looked after themselves					
Is sociable					
Helped clear people away from a suspect package found in an airport					
Has education and intelligence					
Once refused to give money to help starving people in Ethiopia					
Shows emotional stability and maturity					
Once cared for a stray dog injured by a car					
Has no prior sexual experience					
Got out of helping at a children's Christmas party					
Has a similar political background to me					
Did not mind being thought a coward by refusing to help other people					
Has a pleasing disposition					
Volunteered to help out in a local hospital					
Is a good cook and housekeeper					
Had a pet put down rather than pay the vet's bill for an operation					
There is mutual attraction - love					
Climbed a tree to rescue a neighbour's cat					
Has a desire for home and children					

APPENDIX 4.1

MATE PREFERENCES

Below are a list of characteristics and examples of behaviour that you may look for in a husband, wife or partner. Please rate each one according to how undesirable through to how desirable you think they are on the five-point scale below. Take your time and think carefully before placing a tick opposite each of the items.

Items	Undesirable → Desirable				
Has a dependable character					
Is ambitious and industrious					
Occasionally willing to be dishonest if it pays					
Ran the London Marathon to raise money for a good cause					
Is good looking					
Not bothered about being thought stingy towards other people					
Has a similar education to me					
Once dived into a river to save someone from drowning					
Got out of visiting a friend in a hospice					
Enjoys good health					
Donates blood regularly					
Shows refinement and neatness					
Regularly helps an elderly neighbour					
Has good financial prospects					
Once stood by and let someone else rescue children trapped in a burning house					
Has a similar religious background to me					
Volunteered to help without pay on a week’s holiday for people with disabilities					

Item	Undesirable → Desirable				
Has a favourable social status or rating					
Thinks we'd all be better off if everybody looked after themselves					
Is sociable					
Helped clear people away from a suspect package found in an airport					
Has education and intelligence					
Once refused to give money to help starving people in Ethiopia					
Shows emotional stability and maturity					
Once cared for a stray dog injured by a car					
Has no prior sexual experience					
Got out of helping at a children's Christmas party					
Has a similar political background to me					
Did not mind being thought a coward by refusing to help other people					
Has a pleasing disposition					
Volunteered to help out in a local hospital					
Is a good cook and housekeeper					
Had a pet put down rather than pay the vet's bill for an operation					
There is mutual attraction - love					
Climbed a tree to rescue a neighbour's cat					
Has a desire for home and children					

SELF-ASSESSMENT

Please tick the relevant box below that indicates how often, if at all, you have actually carried out the following actions.

	Never	Once	More than once	Often	Very often
I have given directions to a stranger					
I have given change for a banknote to a stranger					
I have given money to a charity					
I have given money to a stranger who needed it or asked me for it					
I have donated goods or clothes to a charity					
I have done voluntary work for a charity					
I have donated blood					
I have helped carry a stranger's belongings (books, parcels, etc.)					
I have delayed a lift and held the door open for a stranger					
I have helped push a stranger's car that had broken down					
I have allowed someone to go ahead of me in a queue (eg in the supermarket, for a photocopier)					
I have given a stranger a lift in my car					
I have pointed out a clerk's error (eg in a bank, at the supermarket) in undercharging me for an item					
I have let a neighbour who I didn't know too well borrow an item of some value to me (eg a dish, tools, etc.)					
I have bought charity Christmas cards deliberately because I knew it was for a good cause					
I have voluntarily helped a workmate or classmate who I did not know that well with a task where my knowledge was greater					
I have, before being asked, voluntarily looked after a neighbour's children or pets without being paid for it					
I have offered to help a handicapped or elderly stranger across a street					
I have offered my seat on a bus or train to a stranger who was standing					
I have helped an acquaintance to move households					

PERSONAL ATTITUDES AND TRAITS

Here are a number of statements about personal attitudes and traits. Read each one and decide whether the statement is true or false as it relates to you.

	True	False
I never hesitate to go out of my way to help someone in trouble		
It is sometimes hard for me to go on with my work if I am not encouraged		
I have never intensely disliked anyone		
On occasion I have had doubts about my ability to succeed in life		
I sometimes feel resentful when I don't get my way		
I am always careful about my manner of dress		
My table manners at home are as good as when I eat out in a restaurant		
If I could get into a movie without paying and be sure I was not seen, I would probably do it		
On a few occasions, I have given up doing something because I thought too little of my ability		
I like to gossip at times		
There have been times when I felt like rebelling against people in authority even though I knew they were right		
No matter who I'm talking to, I'm always a good listener		
I can remember 'playing sick' to get out of something		
There have been occasions when I took advantage of someone		
I'm always willing to admit it when I make a mistake		
I always try to practice what I preach		
I don't find it particularly difficult to get along with loud mouthed, obnoxious people		
I sometimes try to get even, rather than forgive and forget		
When I don't know something I don't at all mind admitting it		
I am always courteous, even to people who are disagreeable		

	True	False
At times I have really insisted in having things my own way		
There have been occasions when I felt like smashing things		
Before voting I thoroughly investigate the qualifications of all the candidates		
I would never think of letting someone else be punished for my wrongdoing		
I never resent being asked to return a favour		
I have never been annoyed when people expressed ideas very different from my own		
I never make a long trip without checking the safety of my car		
There have been times when I was quite jealous of the good fortune of others		
I have almost never felt the urge to tell someone off		
I am sometimes irritated by people who ask favours of me		
I have never felt that I was punished without cause		
I sometimes think when people have a misfortune they only got what they deserved		
I have never deliberately said something that hurt someone’s feelings		

Thank you for completing this questionnaire.

APPENDIX 4.2

Please complete the following details about yourself by ticking the correct box:

1. Gender: Male ☐
Female ☐

2. Are you: A twin ☐
The spouse/partner of a twin ☐

3. Age: ________________

4. Current Marital Status: Single ☐
Married ☐
Divorced ☐
Living with Partner ☐
Separated ☐
Widowed ☐

5. If you are married or are living with a partner what has been the length of your relationship?

_____________Years ____________Months

6. Would you describe yourself as heterosexual? Yes ☐
No ☐

7. Are you a United Kingdom national? Yes ☐
No ☐

8. To which ethnic group would you describe yourself as belonging?

White European ☐
African ☐
Afro-Caribbean ☐
Bangladeshi ☐
Indian ☐
Pakistani ☐
Other Asian ☐
Other ☐

9. In terms of religion would you describe yourself as:

Anglican ☐

Catholic ☐
Other Christian ☐
Agnostic/Atheist ☐

Buddhist ☐

Hindu ☐
Islam ☐
Jewish ☐

Sikh ☐

Other ☐

APPENDIX 4.3

Dear Participant,

We are currently carrying out a study, with a researcher from the University of Nottingham, to measure the preferences we have towards certain behavioural characteristics in a long-term mate (ie husband, wife or partner).

The attached questionnaire asks you to rate the desirability of a range of characteristics and examples of behaviour that you may look for in a mate as well as to respond to some questions designed to measure certain personality traits of your own. Completing this questionnaire is of course entirely voluntary but we have found that most people find it an interesting and enjoyable exercise to do. It could take you about ten minutes. Please think carefully before responding to each item.

<u>However it is essential that you complete the questionnaire on your own, unprompted by your spouse or partner. We need hardly state that collaboration between spouses/partners while completing them would destroy the scientific value of the exercise since responses would not be a true or impartial reflection of your own preferences.</u>

<u>Your response will be treated in the strictest confidence. If you decide to take part in this study please sign below to confirm that you have agreed to participate. Then place your completed questionnaire, including this page, in the envelope provided and post it. There would be no postage cost to you. This page will be separated from the questionnaire on receipt in order to ensure anonymity.</u>

We would finally like to thank you in anticipation of your kind co-operation.

Yours sincerely,

Lynn Cherkas Tim Phillips

I (full name) ____ consent to take part in this survey and understand that the information given will be treated in the strictest confidence and used for the purposes of this study only.

Signed __________________________ Dated _______________

APPENDIX 7.1

Responses To Volunteer Motivation Questionnaire (excluding Responses to the VFI and SRA scale)

1(a) Gender	62 29	Female Male
1 (b) Mean Age (± SE)	39.4 (± s.e. 1.197)	
1 (c)Employment Category	19 50 0 9 4 1 7	Academic Administrative, Professional, Managerial Manual Research Technical Services Other Employee Student
1 (d) How many hours paid work (including overtime) do you carry out on average each week?	4 10 44 33	0 – 10 11 - 29 30 – 39 40 +
1 (e) Marital Status	37 16 29 6 1 2	Married Living with partner Single Divorced Separated Widowed
1 (f) What is your pay rate (i.e. assuming you work full-time for a year)?	3 0 44 40 3	Under £4.000 £4,000 - £9,999 £10,000 - £24,999 £25,000 - £49.999 £50,000 +
1 (g) At what age did you complete your formal education?	0 10 13 66	14 15-16 17-20 21+
2. Are you carrying out any voluntary activity at present?	70 21	Yes No
3. Over what period have carried out any voluntary	33. 7 months	

activity in the past five years (i.e. in years and months)?	(s.e. ± 2.52)	
4. Are you or have you carried out any of this activity as a result of the Active Communities Initiative?	49	Yes
	42	No
5. Describe any voluntary activity carried out as a result of the Active Communities Initiative.	34	Working for/with schoolchildren
	1	Other child/youth oriented activity not involving disability.
	2	Animal welfare.
	2	Adults with disabilities/ elderly.
	2	Arts.
	1	Adult literacy, numeracy.
	7	Local community activity (e.g. redecorating building, helping at sports event).
	1	Working with homeless.
	8	Other or where group helped no clear.
6. Describe any other voluntary activity you are doing at present.	10	Working for/with schoolchildren
	7	Other child/youth oriented activity not involving disability.
	3	Children with disability.
	3	Animal welfare.
	6	Adults with disabilities/ elderly.
	5	Arts.
	3	Adult literacy, numeracy.
	5	Church-based activity (group being helped not specified).
	2	Local community activity (e.g. neighbourhood watch, stewarding).
	2	Territorial Army, Special Constable.
	1	Working with homeless.
	5	Other or where group helped no clear.
7. How many hours voluntary activity have you carried out over the last four weeks?	8.8 hours (s.e. ± 3.325)	
8. Please list below any other reasons you originally had for volunteering that are not covered by the last question. [Only 21	6	Wanted others to enjoy the experience too.
	10	Has been volunteering 'since I was at school'. Desire to put something into local community 'rather than always taking'. *

responses not seen as reflecting 6 motivational functions included. What was seen as ‘egalitarian marked with an *]	17	Experience of own family
	22	Volunteering has ‘some element of payback’ *
	23	‘redistribution of bad fortune’ *
	27	No guilt about being fortunate just a desire to ‘give something back to those less fortunate’. *
	30	Avoidance of boredom
	32	Giving ‘something back to the community’. *
	40	A good environment was ‘an important part of my own upbringing.’
	45	Emphasised volunteering when growing up.
	53	Social justice. *
	60	Admired ‘courage and strength’ of severely disabled children. ‘I feel humbled’.
	61	We are ‘merely stewards of possessions’ best used to help ‘others less fortunate than ourselves’ *
	66	You can’t blame anyone for ills of society if you don’t do something yourself. *
	69	Initially avoidance of boredom but now clients ‘dependent of me’.
	89	Link with activities of own children.
	91	Sense of equity and fairness. *
	92	Volunteered by others
	96	Giving appreciation of music to people with disabilities.
	101	Approached by Church. Link with own children.
	102	Wants children to share love of music.