



## Do humans prefer altruistic mates? Testing a link between sexual selection and altruism towards non-relatives

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Humans are often seen as unusual in displaying altruistic behaviour towards non-relatives. Here we outline and test a hypothesis that human altruistic traits evolved as a result of sexual selection. We develop a psychometric scale to measure mate preference towards altruistic traits (the MPAT scale). We then seek evidence of whether mate choice on the basis of altruistic traits is present and find it in one study ( $N = 170$  couples). We also predict that a stronger female MPAT, as measured by responses to the MPAT scale, will be expressed – a result found in all three studies ( $Ns = 380, 340,$  and  $398$ ). Both sets of results are consistent with the hypothesized link between human altruism towards non-relatives and sexual selection.

### The puzzle of altruism

Altruistic behaviour is a major puzzle in that any genes associated with selfless behaviour are likely to be quickly driven to extinction in the ‘struggle for existence’ proposed by Darwin (1859). Within biology, the current consensus is that altruism towards relatives can be accounted for by it benefiting the altruistic genes that they share (Hamilton, 1963). Altruism towards non-relatives is usually explained by theory based on reciprocity and reputation (e.g. Leimar & Hammerstein, 2001; Trivers, 1971) in which an altruistic act performed by one individual, if reciprocated at a later stage by others, benefits genes linked to this process. Within psychology, models based on altruistic (e.g. empathy), egoistic (e.g. emotional relief) or benevolent (both donor and recipient gain, which does not necessarily involve reciprocity) motives have been suggested to explain helping non-relatives (Batson, 1991; Baumann, Cialdini, & Kenrick, 1981; Ferguson, Farrell, & Lawrence, 2008).

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Here, we outline and test an alternative account of how human altruism towards non-relatives originated that focuses on ultimate causation. We propose that altruistic traits evolved as a result of sexual selection under the special conditions of human evolution.

### ***The sexual selection hypothesis: The evolution of altruism towards non-relatives***

The theory of sexual selection was proposed by Darwin (1859, 1871) who recognized that certain traits observed in nature, such as song, bright colours, crests, horns, and prominent tail feathers, reduced the survival chances of the individuals displaying them, and thus appeared to be at odds with his theory of natural selection. Darwin proposed that these traits survived because they offered advantages under a separate process of sexual selection. Darwin (1871) saw sexual selection taking two forms. The first, since termed intrasexual selection, involves aggressive competition, typically between males, to drive off or kill rivals. The second, since called intersexual selection, involves competition to attract mates, usually females, who then play an active role in choosing a mate on the basis of display of the sexually selected traits (e.g. crests, tail feathers, dance). It is the second form, intersexual selection, that we will concentrate on here.

Zahavi (Zahavi, 1977, 1995; Zahavi & Zahavi, 1997) was the first to suggest that altruistic traits might be linked to sexual selection. He proposed that altruism originated as a 'handicap' that evolved because it gave a 'costly' and therefore accurate 'signal' of the phenotypic and genetic quality of the altruist to others. Zahavi saw 'costly signalling' of altruistic traits as applying to allies and competitors of the same sex as well as other sex mates. Here, we see 'signalling' to potential mates as most likely to promote biological 'fitness' and thus we focus solely on a specific link between sexual selection and altruistic traits.

Various mechanisms have been proposed as to how sexual selection works (Andersson, 1994; Andersson & Simmons, 2006). One mechanism, for example, sees sexually selected traits being favoured because they act as indicators of phenotypic and genetic quality - of which Zahavi's notion of sexually selected traits as 'handicaps' is a prime example (Zahavi, 1975). The 'direct phenotypic benefit' mechanism envisages the sexually selected trait itself as offering an advantage to the female and her offspring (Kirkpatrick & Ryan, 1991). The 'runaway' mechanism envisages genes associated with both mate preference and preferred trait rapidly increasing in frequency as a result of a feedback loop in which the preferred trait becomes ever more attractive until halted by its growing cost under natural selection (Fisher, 1958; Lande, 1981).

What these and other sexual selection mechanisms have in common is the notion of genes associated with (1) a mate preference expressed in one sex towards (2) a preferred trait expressed in the other (Andersson & Simmons, 2006). The effects of genes associated with mate preferences, particularly where selection may have affected females and males differently, should thus be expressed in contemporary populations (Buss, 1989). If the sexual selection hypothesis is valid we would therefore expect to measure the effects of sexual selection on mate preference towards altruistic traits (MPAT) in human populations.

What selection pressures might have favoured the evolution of altruistic traits under human sexual selection? Three linked conditions are suggested: (1) the expansion of the human brain; (2) consequent selection pressure acting on female mate preference; and (3) the evolution of language.

Firstly, the increased size of the prenatal brain is likely to have led to 'premature' birth in relation to the human life-span to help mother and offspring survive (Portmann, 1990). A consequence is that human newborns are more helpless than those of other mammals and thus require an extended period of dependence on parental care. The energy cost of the expanding human brain has been seen as leading indirectly to the necessity for a high-quality diet (Aiello & Wheeler, 1995). 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 other primates (Gangestad, 2007).

Secondly, 'premature' birth and the increased cost of the human brain would have been likely to have led to selection pressures acting on hominid mothers to choose a mate willing, as well as, able to make a substantial and long-term parental investment. In such an environment displays of altruistic behaviour such as caring and generosity towards others and bravery and cooperation on behalf of a group could have acted as reliable and accurate cues for hominid females in selecting such mates. Thus strong selection pressures acting on female MPAT could have ensued with genes associated with both mate preference and preferred trait (i.e. altruism towards non-relatives) increasing in frequency as a result.

Each of the sexual selection mechanisms discussed above has relevance to these putative conditions. Under the 'direct phenotypic benefits' mechanism (Kirkpatrick & Ryan, 1991) a correlation between altruistic traits and a willingness and ability to provide continuing resources and protection to the female and her offspring could have favoured MPAT. Under the 'indicator' mechanism, mate preference towards 'signals' of individual quality associated with altruistic traits (Zahavi, 1977) could have been rewarded under these stringent conditions. Under the 'runaway' mechanism genes associated with MPAT could have increased in frequency with those related to altruistic traits until halted by the increasing cost of displays of altruistic traits under natural selection (Fisher, 1958; Lande, 1981).

Thirdly, the evolution of language and advanced cognition, is likely to have made hominid sexual selection a rigorous and sophisticated process. As a result of the development of language and intelligence 'sexual gossip' (Miller & Todd, 1998) could have become a prominent feature of life in ancestral populations. With 'sexual gossip' reported incidents of altruistic acts such as kindness or cooperation towards non-relatives and bravery and cooperation in defence of a group could have been communicated on a widespread basis and over long time scales. Accurate 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) identified. A further important aspect of 'sexual gossip' is that displays of altruistic traits would not have needed to be confined to overtly mating contexts. 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 even without the immediate stimulus of overt reproductive competition.

These three conditions are therefore likely to have resulted in selection pressures acting on female hominids to choose mates who displayed altruistic traits. As discussed above, these selection pressures in ancestral populations should be evidenced by genes associated with them being expressed differently in females and males in modern humans (Buss, 1989). One can therefore predict that evidence for a stronger female

MPAT should be present in a modern population and that one should expect to find a relationship between this mate preference and altruistic traits in modern mate choices. The challenge is therefore to measure these putative patterns in a modern population.

### **Evidence of a link between sexual selection and altruism**

What evidence is there that altruistic behaviour is linked to sexual selection in the environment in which humans evolved (i.e. Hunter/Gatherer societies)? Anthropological studies (Hawkes, 1991, 1993; Kaplan & Hill, 1985) have found that there is little relationship in modern Hunter/Gatherer societies between the amount of game acquired by Hunters and how much they and their families actually consume. Why then do successful Hunters pursue a less biologically 'fit' (and, by implication here, altruistic) strategy in consistently providing a disproportionately large supply of hunted meat to their groups of mostly non-relatives at greater cost and risk to themselves? It has been found that successful Hunters (and, by implication, here successful altruists) enjoy greater reproductive access to females (Hawkes, 1991; Hawkes, O'Connell, Hill, & Charnov, 1985; Hill & Hurtado, 1996; Hill & Kaplan, 1988; Kaplan & Hill, 1985; Smith, 2004) and their offspring enjoy higher survivorship rates (Hawkes, 1991; Hill & Kaplan, 1988; Hill & Hurtado, 1996; Kaplan & Hill, 1985). This evidence is thus consistent with sexual selection favouring the biological 'fitness' of successful altruists.

### **Distinctiveness of this research**

There is evidence that human mate choice favours characteristics similar to altruism. 'Considerate', 'honest', 'affectionate', 'dependable', 'kind', and 'understanding' were rated among the ten most valued characteristics in a mate (out of 76 characteristics), with females preferring these characteristics significantly more than males (Buss & Barnes, 1986). 'Kind and understanding' was ranked as the most desired characteristic in a cross-cultural study ( $N = 9,474$ ) (Buss *et al.*, 1990). Females expressed significantly greater preference towards 'expressive' (i.e. 'affectionate, compassionate') mates (Howard, Blumstein, & Schwartz, 1987) while women were found to rate prosocial men as more attractive in another study (Jensen-Campbell, Graziano, & West, 1995).

Here we define altruism as any act that increases the chances of survival or reproductive success of another individual at the expense of that of the altruist (Ridley & Dawkins, 1981). This definition differentiates it from the characteristics described above in that the altruist must incur a real or potential cost to biological fitness. This occurs in terms of personal risk or through diversion of time and effort to non-relatives that, in an evolutionarily appropriate context, would have reduced biological fitness. As such, this definition encompasses the construct of 'heroism', which was differentiated from 'altruism' in a comparable study (Kelly & Dunbar, 2001). In contrast, the characteristics described above need not incur this cost to biological fitness (i.e. reduction in the chances that genes associated with the behaviour will be represented in subsequent generations). The current research therefore makes a distinctive contribution to the literature but one based on a widely recognized definition of altruism.

### **Objectives**

Earlier we explained why selection pressures acting on MPAT in ancestral populations might be evidenced in modern humans. To explore this possibility, we developed a

psychometric scale - the MPAT scale - using a sample of students ( $N = 380$ ). We predicted that evidence of mate choice on the basis of altruistic traits would be found and this prediction was examined in a sample of spouses and partners ( $N = 170$  couples) in Study 2. We also predicted that stronger female MPAT (as measured by the MPAT scale) would be present in a modern population. This was assessed in Studies 1 ( $N = 380$ ), 2 ( $N = 340$ ), and 3 ( $N = 398$ ), which contained samples of contrasting mean age.

### **STUDY 1: DEVELOPMENT OF MATE PREFERENCE TOWARDS ALTRUISTIC TRAITS (MPAT) SCALE**

This study was concerned with developing a psychometric scale to measure the MPAT scale, as no suitable existing scale was found. Initial data on the reliability (internal consistency and test-retest reliability) and validity are presented. Construct validity was tested by correlating responses to the MPAT scale with those towards psychometric scales that measure similar constructs (i.e. 'altruistic personality' and mate preference). A test of sex differences in response to the MPAT scale was also carried out.

#### **Methods**

##### **Sample**

A sample of university students was used ( $N = 380$ ; 49% female) with a mean age of 19.4 years ( $\pm SE$  0.065).

##### **Procedure**

A focus group of seven undergraduate and postgraduate students was convened to derive examples of altruistic behaviour in a potential mate. These examples were then refined through interviews with a further 14 participants. Fifty-one items were identified and these were administered to the sample. Participants were asked to rate the relative desirability of each item in someone with whom they would like to have a relationship (i.e. 'a future husband, wife, boyfriend, girlfriend') using a 5-point Likert-type scale (0-4) to reflect low through to high desirability.

To eliminate items that discriminated poorly between responses, the skewness of each item was measured by dividing the coefficient of skewness by its standard error and items with resulting values greater than two were discarded (cf. Ferguson & Cox, 1993). Items were also measured for kurtosis and those with values greater than two were also removed. In addition, items were assessed on grounds of whether they met the criterion of gender neutrality. The remaining items were subjected to principal components analysis (Kline, 1994). Internal consistency was assessed using Cronbach's coefficient alpha ( $\alpha$ ) while the test/retest reliability of the new scale was measured over a 14-21 day period using a sample of university students ( $N = 52$ ; 71% female; mean age = 19.6 ( $\pm SE$  0.19) years).

##### **Measures**

The construct validity of the MPAT scale was assessed by correlating responses to it with those towards measures of mate preference and 'altruistic personality'. A scale designed to measure mate preferences towards 18 characteristics in a potential mate (e.g. 'good looks', 'good financial prospect') has been used widely in similar studies (e.g. Buss,

1989; Hill, 1945). Referred to here as the general mate preference (GMP) scale, it requests participants to rate the importance or desirability of the characteristics on a 4-point Likert-type scale and is employed in Studies 1–3. Its internal consistency, as measured by Cronbach's coefficient  $\alpha$ , was .72 in this study and .82 and .72, respectively in Studies 2 and 3. The Self-Report Altruism (SRA) scale (Rushton, Chrisjohn, & Fekken, 1981) was designed to measure the 'altruistic personality' of the participant and is employed in Studies 2 ( $\alpha = .82$ ) and 3 ( $\alpha = .81$ ).

## Results and discussion

Thirty-four items with unacceptable values of skewness and kurtosis were removed and one item was taken out on the grounds that it was thought insufficiently gender neutral. The remaining 16 items were then subjected to principle components analysis. While four factors with eigenvalues greater than 1.0 were identified (4.13, 1.41, 1.30, and 1.15), the scree plot indicated that a one - component solution was most appropriate.

Items with communalities below 0.30 (Kline, 1998, p. 58) were removed and the analysis rerun. For the remaining nine items, the KMO measure of sampling adequacy (0.87) was excellent (Field, 2005) and the Bartlett's test of sphericity was significant ( $p < .001$ ), indicating that the data were factorable. Again, the scree test suggested a single factor model with only one eigenvalue greater than one (3.71) accounting for 41.22% of the variance. The component matrix of the resulting nine items that formed the MPAT scale is shown in Table 1.

**Table 1.** Principle components analysis: matrix of items of 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

## Reliability and validity analyses

The coefficient  $\alpha$ s of the MPAT scale were .82, .84, and .83 in Studies 1–3, respectively, well exceeding the minimum level considered necessary in each case (Oppenheim, 1992; Loewenthal, 1996) while the MPAT scale's test/retest reliability demonstrated that the scale was temporally stable ( $r_{50} = .76, p < .01$ ). Support for the construct validity of the new scale was provided by the positive significant correlations found between responses to it and those towards established measures of mate preference and altruistic traits in the studies where they were used (see Table 2). We also present values where the correlations were corrected for unreliability, showing in all cases larger coefficients, thus reinforcing the construct validity found (see Table 2).

**Table 2.** Construct validity of MPAT scale in Studies 1–3

Scales	Study 1 (N = 380)		Study 2 (N = 170 couples)		Study 3 (N = 398)	
	Uncorrected	Corrected	Uncorrected	Corrected	Uncorrected	Corrected
GMP	$r_{343} = .11, p = .052$	$r_{343} = .14$	$r_{298} = .36, p < .001$	$r_{298} = .43$	$r_{377} = .35, p < .001$	$r_{377} = .45$
SRA	–	–	$r_{326} = .17, p = .002$	$r_{326} = .21$	$r_{390} = .16, p = .002$	$r_{390} = .19$

Note. GMP, general mate preference scale; SRA, self-report altruism scale. Uncorrected coefficients = raw correlation coefficients, Corrected coefficients = corrected for degree of unreliability in each measure.



### **Sex differences in response to MPAT scale**

A stronger female response was found to the MPAT scale (mean female score = 23.81;  $\pm$  SE 0.305, mean male score = 22.51;  $\pm$  SE 0.312). This sex difference was significant ( $t_{366} = 2.99$ ,  $p = .003$ ; Cohen's  $d = 0.31$ ), a finding consistent with the proposed hypothesis.

## **STUDY 2: MATE CHOICE ON THE BASIS OF ALTRUISTIC TRAITS**

The objective of this study was to test whether mate choice on the basis of altruistic traits is present in a sample of couples, a process consistent with sexual selection acting on them. A sample of participants who had already made a choice of long-term mate (i.e. husbands, wives or partners in long-term relationships) was obtained and the MPAT of one spouse (as measured by the MPAT scale) correlated with a measure of 'altruistic personality' in the other (Rushton *et al.*, 1981). A test of whether mate choice on the basis of altruistic traits was present was thus provided. A test of sex differences in responses to the MPAT scale was also carried out.

Altruism is an aspect of human behaviour that is likely to be heavily influenced by social norms and there is thus a danger that the resulting self-report data might reflect what is considered culturally acceptable or socially desirable rather than be the accurate and 'true' responses of the participants themselves. Fortunately, this problem has long been recognized by practitioners in the field and can be statistically controlled for by using a social desirability (SD) scale (Crowne & Marlowe, 1964), although this is not a foolproof method (Piedmont, McCrae, Riemann, & Angleitner, 2000).

Another possible confounding variable is that the responses of spouses might have become more alike as a result of their living in close proximity for much of their lives - rather than reflecting what determined their original mate choice. An ideal solution to this problem would have been to conduct the study at the time when the mate choice was made but, as this was not practicable, participants were asked to report the length of their relationship so that the effect of this variable on responses could be measured.

Finally, human mating decisions typically involve mutual choice and so there will be an inevitable degree of non-independence between the choices of spouses. This raises the statistical problem of pseudo-replication whereby data are double-counted, thus falsely inflating the value of  $N$ . To address this problem, the sample was also divided into two subsamples - firstly, in which female MPAT scores were correlated with male SRA scores and, secondly, male MPAT scores with female SRA scores. In Study 2 the following prediction was tested:

*Prediction 1:* That MPAT in one spouse/partner, as measured by the MPAT scale, will correlate significantly with a measure of 'altruistic personality' in the spouse/partner chosen, after the effects of SD, pseudo-replication and the length of relationship have been taken into account.

## **Methods**

### **Sample**

A sample of participants who reported themselves as being married or in long-term relationships was used ( $N = 340$ ), having a mean age of 57.9 ( $\pm$  SE 0.69) years.



### **Procedure**

To ensure that participants were blind to the prediction being tested, the nine items of the MPAT scale were included at random with the 18 items of the GMP scale under the heading 'mate preferences'. Participants were informed that it was a study of the characteristics they found attractive in a potential mate and asked to rate each item on the basis of its desirability on a 5-point Likert-type scale. Altruistic traits were not mentioned. The questionnaire also included a measure of self-reported altruism under the heading 'self-assessment' to disguise its purpose and a measure of SD responding under the heading 'personal attitudes and traits'. A page requesting personal details including gender, age, marital status and length of relationship was also included.

The questionnaire was administered to participants attending sessions organized by the Twin Research and Genetic Epidemiology Unit, based at St Thomas's Hospital, London, UK, where a range of other unrelated scientific studies were also carried out. In cases where participants indicated that they had a current spouse or partner they were handed two questionnaires - one to complete themselves at the time and one to take home to their spouse or partner for that person to complete and return by Freepost. In the vast majority of cases participants who attended the sessions completed the questionnaire there and then. They were urged verbally and in writing not to try to influence the responses of their spouses/partners when these subsequently completed the questionnaire.

### **Measures**

#### *Self-report altruism (SRA)*

The SRA scale (Rushton *et al.*, 1981) was employed which requests participants to rate the frequency with which they have performed 20 altruistic acts (i.e. never, once, more than once, very often). Minor changes were made to reflect the different culture and time in which the scale was to be used (e.g. 'photocopier' was substituted for 'Xerox machine', 'lift' for 'elevator'). The coefficient  $\alpha$  in this study was .82.

#### *Social desirability (SD)*

The Marlowe-Crowne SD scale (Crowne & Marlowe, 1964) was employed which presents participants with a list of 33 culturally acceptable but probably untrue statements (e.g. 'I am always courteous, even to people who are disagreeable') in a true/false format. Thus the extent to which participants favoured socially desirable, but probably incorrect statements of their true response were measured. Responses to the SD scale could thus be used to control for any effects of SD on the correlation between MPAT and SRA scale scores. The coefficient  $\alpha$  in this study was .82.

#### *Mate preference towards altruistic traits (MPAT) and the general mate preference (GMP) scale*

MPAT and GMP were employed using the same scales described in Study 1. In this study the coefficient  $\alpha$  was .84 for the MPAT and .82 for the GMP scale.

### **Data analysis**

Prediction 1 was initially tested by examining correlations between one spouse/partner's response to the MPAT scale and the other's response to the SRA scale while controlling for SD and length of relationship. To guard against potential

pseudo-replication effects separate analyses of the association between (1) female MPAT and male SRA and (2) male MPAT and female SRA scale scores were conducted. Length of relationship was also controlled for in these two subsamples. To provide an additional perspective, moderated regression analysis was also employed to explore whether there were any effects of relationships of varying length in these two subsamples. The method was based on procedures outlined by Aiken and West (1991).

Finally, sex differences in response to the MPAT scale were examined. The effect size of the sex difference in response to the MPAT scale in Study 1 was used ( $d = 0.31$ ) to estimate the minimum sample size required here to achieve power of 0.80 with a  $p$  value of .05 (two-tailed) (Cohen, 1992). Using ZUMASTAT (Jaccard, 2006) this was found to be 158 females and 158 males. As the numbers of female and male participants were  $N = 168$  and  $N = 170$ , respectively the sample size obtained was adequate. Analysis of covariance (ANCOVA), using SRA and SD scores as covariates, was employed to explore whether a stronger female MPAT was present.

Occasionally participants failed to respond to a particular item. Substitution of missing items with the mean score of that participant for all other items in response to the scale is one solution to the loss in statistical power (Oppenheim, 1992, pp. 279–281) and has been employed elsewhere (e.g. Moore, Cassidy, Smith, & Perrett, 2006; Rushton & Bons, 2005). Mean substitution was used sparingly (i.e. where no more than one item was missing in the MPAT scale, no more than two items in the 20-item SRA scale and no more than three items in the 33-item SD scale).

## Results and discussion

Of those who attended the sessions over two-thirds (69%) reported that they had spouses or long-term partners and had spouses/partners who subsequently returned the completed and returned questionnaire.

### **Correlation between MPAT and SRA scale responses in partners**

The correlation between the scores of one spouse/partner in response to the MPAT scale and the other in response to the SRA scale and vice versa was found to be significant ( $r_{324} = .18, p = .001$ ). When length of relationship was controlled for the correlation remained significant ( $r_{293} = .16, p = .006$ ), as it did when SD was controlled for ( $r_{305} = .15, p = .008$ ).

When the two subsamples (i.e. female MPAT-male SRA scores and male MPAT-female SRA scores) were examined a significant set of correlations were obtained (i.e.  $r_{163} = .20, p = .011$  and  $r_{161} = .16, p = .045$ , respectively). These two correlation coefficients were not significantly different from each other ( $z = 0.36, p = .71$ ). When length of relationship was fitted as a covariate the first order partial correlations between MPAT and SRA scale scores were found to be significant and the same in both subsamples ( $r_{150} = .17, p < .05$ ). Prediction 1 was thus supported.

Moderated regression analyses were then used to examine in further detail whether length of relationship moderated the association between MPAT and SRA scale scores. MPAT scale scores acted as the dependent variable and SRA scale scores and length of relationship were entered at Step 1 and their cross-product term at Step 2. All predictor variables were centred prior to the analyses (Aiken & West, 1991).

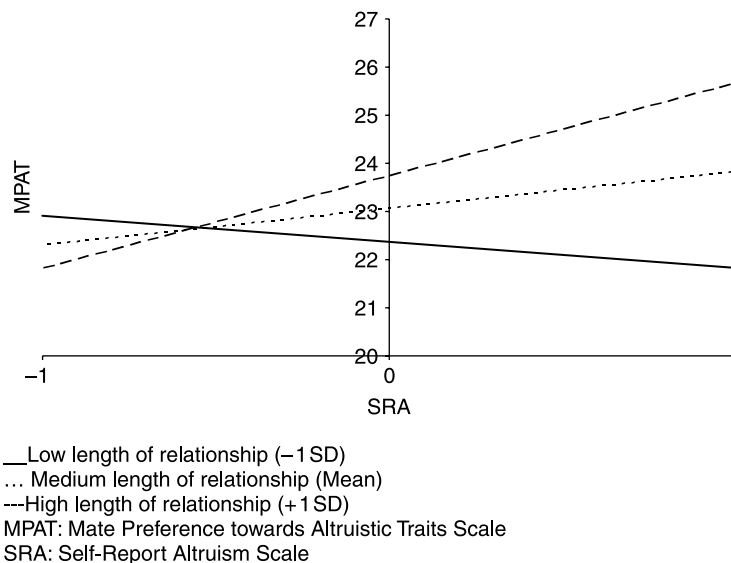
The male MPAT and female SRA analysis displayed no significant effects at any stage in relationship length. No significant effects were found at either Step 1 or 2 (Step 1:  $p = .11$ ; Step 2:  $p = .12$ ). At Step 1, the MPAT-SRA association was significant ( $\beta = 0.17$ ,  $p = .037$ ), but the effect of relationship length was not, or was the MPAT-SRA relationship moderated by relationship length ( $\Delta R^2 = .009$ ,  $p = .23$ ,  $\beta = 0.09$ ,  $p = .23$ ).

In the other analysis a rather different picture emerged (see Figure 1). The association between female MPAT and male SRA scale scores indicated significant effects at Step 1 ( $R^2 = .41$ ,  $p = .043$ ), showing that female MPAT and male SRA scale scores were significantly associated ( $\beta = 0.17$ ,  $p = .041$ ) but with no association for relationship length ( $\beta = 0.08$ ,  $p = .31$ ). Importantly the interaction term added significantly to the equation ( $\Delta R^2 = .04$ ,  $p = .014$ ,  $\beta = 0.20$ ,  $p = .014$ ). Simple slope analysis (Jaccard, 2006) showed that the MPAT-SRA association was non-significant for both low levels ( $-1$  SD) of relationship length ( $t_{149} = 0.55$ ,  $p = .58$ ,  $B = -0.39$ ) and moderate levels of relationship length ( $t_{149} = 1.7$ ,  $p = .10$ ,  $B = 0.47$ ). However, the MPAT-SRA association was significant for high ( $+1$  SD) levels of relationship length ( $t_{149} = 3.2$ ,  $p = .0016$ ,  $B = 0.60$ ).

These various analyses demonstrated that the greater the preference for altruistic traits in a mate the greater the 'altruistic personality' self-reported by the spouse/partner actually chosen. The possibility that these significant associations could be explained by the influence of length of relationship was not supported by moderated regression analysis in one analysis and only partly supported in the other. We conclude that, overall, there are good grounds for seeing evidence consistent with mate choice on the basis of altruistic traits in these results.

### Sex differences in responses to MPAT scale

The mean female score in response to the MPAT scale was 23.31 ( $\pm SE$  0.462) and the male score was 20.49 ( $\pm SE$  0.487). The ANCOVA demonstrated that sex had exerted



**Figure 1.** Interaction of responses to SRA scale and length of relationship on MPAT scale: female MPAT-male SRA analysis.

a significant effect on responses to the MPAT scale (Cohen's  $d = 0.46$ ) (see Table 3). Thus where the effects of 'altruistic personality' and SD were controlled for, females still expressed a significantly stronger mate preference towards altruistic mates in line with the proposed hypothesis.

**Table 3.** ANCOVA of sex differences in response to MPAT scale (Study 2)

Term	$F$ ( $df$ )	$p$
SRA*	10.724 (1, 323)	.001
SD	0.146 (1, 317)	.703
Sex*	17.835 (1, 323)	<.001

Note. SRA, self-report altruism scale; SD, social desirability scale.

\*Indicates terms in minimum adequate model.

### STUDY 3: SEX DIFFERENCES IN MATE PREFERENCE

The sex difference in response to the MPAT scale reported in Study 2 was, however, found in a sample with a mean age of 57.9 years. In the evolutionary scenario proposed above the mean age at which such mate preferences would have been expressed is likely to have been far lower, given probable life expectancies in ancestral populations compared with those in a modern industrial society. The sample used in Study 1, although of more suitable mean age (19.4 years), did not include the SRA or SD scales and was not designed primarily to evaluate sex differences in response. It was therefore essential that we employed an appropriately aged sample to evaluate sex differences in MPAT that could also allow for the possibility that the participant's own 'altruistic personality' or tendency to give a socially desirable response might account for any stronger female response. In Study 3 the following prediction was therefore tested:

*Prediction 2:* A significantly stronger female MPAT, as measured by the MPAT scale, will be found in a sample whose mean age is likely to reflect that of the proposed evolutionary scenario, after the effects of 'altruistic personality' and SD have been taken into account.

### Methods

#### Sample

In Study 3 a sample of mostly university students was used ( $N = 398$ ; 47% female) with a mean age of 19.4 years ( $\pm SE$  0.10). Given the need for a minimum sample size of 158 females and males discussed above, the obtained sample size of  $N = 187$  females and  $N = 211$  males was seen as satisfactory.

#### Procedure

A similar questionnaire to that employed in Study 2 was administered to a sample of mostly university students, with participants again being blind to the prediction tested. An ANCOVA model was used with MPAT scores ( $\alpha = .83$ ) as the dependent variable, sex as the fixed factor and SRA and SD scores as covariates. The coefficient  $\alpha$ s in this study for the SRA, SD, and GMP scales were .81, .74, and .72, respectively. As the standardized residuals were not normally distributed the MPAT scale data were

transformed by squaring and the ANCOVA rerun. 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.

## Results

### Sex differences

The average female response to the MPAT scale was 21.24 ( $\pm SE$  0.384) and the male score 20.04 ( $\pm SE$  0.332). The ANCOVA revealed a significant sex difference in response (see Table 4) although the effect size was small (Cohen's  $d = 0.24$ ) (Cohen, 1992). This result could not be explained solely by the effect of 'altruistic personality' or SD and so Prediction 2 was supported.

**Table 4.** ANCOVA of sex differences in response to MPAT scale (Study 3)

Term	$F$ ( $df$ )	$p$
SRA*	10.481 (1, 387)	.001
SD	2.541 (1, 380)	.112
Sex*	6.547 (1, 387)	.011

Note. SRA, self-report altruism scale; SD, social desirability scale.

\*Indicates terms in minimum adequate model.

## GENERAL DISCUSSION

In this research we present two lines of evidence to explore the hypothesis that human altruistic traits evolved as a result of sexual selection. Firstly, degree of MPAT was found to correlate significantly with degree of 'altruistic personality' in the spouse/partner chosen. This evidence is consistent with a condition necessary for sexual selection to take place - mate choice on the basis of altruistic traits. Secondly, we present evidence of stronger female MPAT, which is in line with what is predicted by the evolutionary scenario outlined in the introduction. Female participants responded significantly more positively to the MPAT scale across the three studies employed ( $N = 1,118$ ). In two of these (2 and 3), which included samples of contrasting mean age, participants' own 'altruistic personality' and SD were included in the study design but were not found to account for the stronger female mate preference found.

Why are these results important? Firstly, the sexual selection hypothesis offers an alternative and largely unexplored approach to solving the major puzzle of altruism towards non-relatives, at least with regard to humans. Secondly, sexual selection has been seen as playing an important role in human evolution, leading to the development of many distinctively human traits (Darwin, 1871; Miller, 2000). Such speculation is, however, not always easy to test empirically. Here, we provide evidence that one distinctive human trait - altruism towards non-relatives - was sexually selected.

The interpretation made here of a link between altruism and sexual selection can be challenged on four possible grounds - (1) a sociocultural account of these results offers a more plausible explanation, (2) the sexual selection hypothesis apparently fails to

account for examples of female altruistic behaviour, of which there is abundant evidence (Becker & Eagly, 2004), (3) the data may be inaccurate as they are self-reported, and (4) the effect size of the sex difference in mate preference in the sample of participants of reproductive age was of small magnitude (Cohen, 1992).

Firstly, altruistic behaviour in many societies is influenced strongly by social norms and is often prescribed on grounds of gender. For example, in Eagly and Crowley's (1986) 'social role theory of gender' females are seen as typically displaying 'nurturant and caring' and males 'heroic and chivalrous' 'helping behaviour'. If participants were influenced by these social norms when responding to the MPAT scale then any association with perceived female or male roles could have skewed responses and possibly led to the results found. However, re-examination of the nine items of the MPAT scale in terms of whether they imply the sex roles proposed by Eagly and Crowley (1986) suggests an approximately equal balance between perceived 'female' and 'male' roles in 'helping behaviour'. Thus the overall effect of the MPAT scale is seen as broadly gender-neutral and unlikely to have skewed responses sufficient to produce the consistently stronger female response.

Another sociocultural interpretation of these results could be based on the 'structural powerlessness' model (e.g. Moore *et al.*, 2006; Wallen, 1989) whereby females are seen as having relatively limited access to power and resources in society. In such an environment signs of a willingness to share power and resources, as evidenced by altruistic behaviour in a mate, might account for the stronger female MPAT found. This interpretation could be the subject of further study to test whether females with greater access to power and resources display a correspondingly lower MPAT.

Secondly, sexually selected traits are typically displayed in one sex but are absent or in a truncated form in the other (Darwin, 1871). It has been proposed that this pattern is related to the relative level of parental investment that each sex makes in its own offspring (Trivers, 1972, 1985). The sex making the larger parental investment (usually females) has, as a consequence, a limit imposed on the number of offspring each can successfully raise in a lifetime. In contrast, for the sex making the smaller parental investment, the level of reproductive success each can potentially enjoy is much higher, leading to more intense reproductive competition between them. Consequently males more usually display traits associated with intersexual selection. This theory is supported in species where the usual male/female sex roles are reversed (Trivers, 1972, 1985) and where it is females who display traits associated with intersexual selection. Importantly, in species where each sex makes a similar level of parental investment, both sexes have been shown to display sexually selected traits (Jones & Hunter, 1993).

The scenario outlined in the introduction suggests a growing level of parental investment being required by *both* sexes in human evolution. Although females in the modern world are often seen as the sex that makes the heavier parental investment (Buss & Schmitt, 1993), human males still typically make a larger parental investment than that of other mammals (Kenrick *et al.*, 1990). While accurate measurement of parental investment raises considerable problems (e.g. Clutton-Brock & Vincent, 1991; Knapton, 1984), the anthropological literature indicates that males in Hunter/Gatherer societies provide an average of 66% of foods (Kaplan, Hill, Lancaster, & Hurtado, 2000) and a similar proportion of calories in foraging societies (Gangestad, 2007). Thus, in terms of food consumption, males make a substantial parental investment in an environment similar to that in which humans evolved.

If we accept Trivers's (1972, 1985) proposal that more equal parental investment between the sexes leads to forms of mutual sexual selection then the data gathered here



is consistent with that logic. No significant sex difference was found in responses to the measure of 'altruistic personality' where it was employed (i.e. Studies 2 and 3). Formal modelling of this argument would help to clarify it further and, if supported, the sexual selection hypothesis could come to be seen as consistent with evidence of altruistic traits in both sexes (Becker & Eagly, 2004).

Thirdly, a limitation to the evidence presented here is that it is based entirely on self-report data. Such data has been criticized on grounds that they are open to biases (Feingold, 1992), particularly in the context of comparing female and male responses (Zohar & Guttman, 1989), and should therefore not be taken at face value (Batson, 1991). Considerable effort was made to maintain the accuracy of the data. Tests of the reliability and validity of the MPAT scale were carried out, although these need to be continued in further studies, particularly involving tests of convergent/discriminant validity. The SD scale was employed to guard against exaggeration due to SD, although this is not a foolproof method (Piedmont *et al.*, 2000). Responses to the MPAT scale were also found to correlate, as predicted, with those towards another self-report measure (the SRA scale), suggesting that both psychometric scales performed their intended functions. However, the possibility remains that some unknown systematic bias might have accounted for the results obtained. In defence, it should be made clear that all measurement of behaviour presents some methodological problems for the researcher. The answer lies in testing the sexual selection hypothesis presented here by using alternative methodologies that do not rely on self-report data.

Finally, the effect size of the sex difference in mate preference in the sample of participants of reproductive age was found to be of small magnitude ( $d = 0.24$ ) (Cohen, 1992). Some may infer that this suggests only a negligible impact in biological terms. Yet over evolutionary time scales female choice can have considerable consequences even when the effect on offspring survivability is relatively minor (Møller & Allatolo, 1999). The pattern of stronger female MPAT found in all three studies was seen as consistent with evidence inferred from the anthropological literature, discussed above, of female choice favouring males who display such traits.

The evidence presented here of a link between sexual selection and human altruism towards non-relatives offers an exciting new insight into a major evolutionary puzzle. Despite a great deal of theoretical work being devoted to understanding altruism over the past three decades this link has remained under-explored. We conclude that the sexual selection hypothesis deserves to be seen as an important and promising new area for future research.

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