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Kinship and altruism: A cross-cultural experimental study

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Humans are characterized by an unusual level of prosociality. Despite this, considerable indirect evidence suggests that biological kinship plays an important role in altruistic behaviour. All previous reports of the influence of kin selection on human altruism have, however, used correlational (rather than experimental) designs, or imposed only a hypothetical or negligible time cost on participants. Since these research designs fail either to control for confounding variables or to meet the criteria required as a test of Hamilton's rule for kin selection (that the altruist pays a true cost), they fail to establish unequivocally whether kin selection plays a role. We show that individuals from two different cultures behave in accordance with Hamilton's rule by acting more altruistically (imposing a higher physical cost upon themselves) towards more closely related individuals. Three possible sources of confound were ruled out: generational effects, sexual attraction and reciprocity. Performance on the task however did not exhibit a perfect linear relationship with relatedness, which might reflect either the intrusion of other variables (e.g. cultural differences in the way kinship is costed) or that our behavioural measure is insufficiently sensitive to fine-tuned differences in the way individuals view their social world. These findings provide the first unequivocal experimental evidence that kinship plays a role in moderating altruistic behaviour. Kinship thus represents a baseline against which individuals pitch other criteria (including reciprocity, prosociality, obligation and a moral sense) when deciding how to behave towards others.

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Recent research, using small-scale experiments based on standard game formats from economics, has shown that people often apply criteria of fairness to social interactions, accede to social pressure and engage in 'altruistic punishment' (punishment that incurs a benefit to the community as a whole, but at a cost to the punishing individual: Fehr & Fischbacher, 2004; Fehr, Fischbacher, & Gächter, 2002; Fehr & Gächter, 2000, 2002; Gintis, Bowles, Boyd, & Fehr, 2003; Orstrom, Gardner, & Walker, 1994). Humans are thus characterized by an unusual level of prosociality: individuals are, in general, willing to adhere to social norms of behaviour delineated by their community, even though they may incur personal costs by doing so.

These kinds of prosocial predispositions are however set into a complex background of more explicit biological interests and social obligations (e.g. those established by the customary modes of the society). Indeed, even in these micro-economic tests, individuals were not immune to the costs of altruism: when the costs to the punisher increased, the frequencies of altruistic punishment declined (Fehr & Gächter, 2002). More importantly, however, even though kinship provides an important strand of the social nexus within which any prosocial behaviour is necessarily embedded, it has been explicitly excluded from all of these studies (as is conventional in micro-economic experiments).

Altruistic behaviour originally proved difficult to explain in evolutionary terms: in a simple Darwinian world, any gene promoting altruism should be rapidly driven to extinction. The solution was provided by Hamilton (1964; popularized by Dawkins, 1976), who showed that evolution occurs as the result of copies of genes being propagated, and that the replication of genes into future generations can occur through either personal reproduction or the reproduction of individuals carrying the same gene(s). Formally known as Hamilton's rule of kin selection, Hamilton's core finding was that a gene for altruism can evolve in a population, providing:

$$rB > C$$

where B is the benefit to the recipient, C the cost to the altruist (both measured as the number of offspring gained or lost) and r the coefficient of relationship (i.e. the probability that they share the same gene by descent). In essence, altruism evolves when the altruist's actions allow it to contribute more copies of its genes to future generations by enabling a relative to reproduce more successfully than by reproducing itself. In effect, when all else is equal, more closely related individuals should be favoured over less closely related individuals. While the currency in Hamilton's (1964) technical definition of altruism is fitness (for which even reproductive success is only a proxy), this cannot easily be measured directly in most real-world studies; most studies of altruism in animals have therefore used as an *operational* definition, the expenditure of energy or resources that may increase the welfare of one individual at the expense of another (Barash, 1977; Dawkins, 1989).

Hamilton's rule has been a foundation stone of modern evolutionary biology and the study of animal behaviour for nearly half a century (e.g. Sober & Wilson, 1998), and there is widespread observational and experimental evidence of its role in moderating altruistic behaviour in non-human animals (e.g. Cheney & Seyfarth, 1990). There is also abundant evidence that humans behave more altruistically towards closer than towards more distant relatives. In societies reliant on subsistence agriculture, cooperation between farmers is twice as likely between relatives as non-relatives (Berté, 1988;

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Hames, 1987). In industrial societies, beneficiaries of a will tend to receive slices of the deceased's estate that are broadly proportional to their genetic relatedness, *r*, to the deceased (Smith, Kish, & Crawford, 1987). Similarly, kinship patterns correlate with: willingness to murder political rivals and form stable alliances (Dunbar, Clark, & Hurst, 1995; Johnson & Johnson, 1991), taking sides in disputes (Chagnon & Bugos, 1979; Hughes, 1988), emotional and material support within social networks (Barber, 1994; Berté, 1988; Betzig & Turke, 1986; Dunbar & Spoors, 1995; Hames, 1987; Hill & Hurtardo, 1996), cooperation under catastrophic circumstances (Grayson, 1993; McCullough & Barton, 1991) and combat situations (Shavit, Fischer, & Koresh, 1994), the coherence and fission of cohabitational units (Chagnon, 1981; Hurd, 1983; Koertvelyessy, 1995), membership of cooperative labour units (Morgan, 1979), exchange of information among US inshore fishermen (Palmer, 1992), safeguarding against infanticide (Hill & Hurtado, 1996) and the investment tendencies of both parents (Chagnon, 1992; Firth, 1957; Hill & Kaplan, 1988) and more distant kin (Euler & Weitzel, 1996; Gaulin, McBurney, & Brakeman-Wartel, 1997; Hawkes, O'Connell, & Blurton-Jones, 1989; Hill & Hurtado, 1996; Pashos, 2001). Finally, across most societies, women are far more likely to provide child care for their relatives than for unrelated neighbours (Bereczkei, 1998; Burton, 1990; Ivey, 2000; Judge, 1995; Pennington & Harpending, 1993; Silk, 1990; Stack, 1975).

While these findings are interesting, all these studies suffer one common drawback: the evidence is entirely observational. In no case is it possible to exclude categorically *all* confounding variables (interaction time, reciprocity, etc.), so as to make an unequivocal test of the claim that human altruistic behaviour is modulated by the genetic relatedness, when other factors are held constant. An exception to this was an experiment reported by Caporeal, Dawes, Orbell, and van de Kagt (1989), who found that individuals were more likely to donate their fee for participating to a local charity when doing the experiment in groups than alone. Although interpreted as evidence for a natural tendency to behave altruistically, thus posing a challenge to Hamilton's rule, the experiment suffered from design flaws (principally, failure to impose a cost) sufficient to compromise the significance of its findings. A similar criticism applies to the experimental studies of prosociality by Fehr and colleagues (Fehr & Fischbacher, 2004; Fehr *et al.*, 2002; Fehr & Gächter, 2002; Gintis *et al.*, 2003): none meet the crucial criterion necessary for a formal test of Hamilton's rule (that the altruist pays a personal cost). Although it might be suggested that participants incur a cost by forgoing their fees, this provides only for a very weak form of altruism because the experiment is cost-neutral to the altruist (who leaves in the same state as he/she arrived, apart from a trivial loss of time). More importantly, because each of these experiments focuses on altruism among unrelated individuals, none provide an experimental test of Hamilton's rule in humans.

In contrast, self-reported frequencies of giving and receiving assistance (financial, emotional, etc.) from female residents in the US suggested that in times of need closer kin were a weightier source of assistance than more distant kin and non-kin (Essock-Vitale & McGuire, 1985). This survey, however, relied on self-reports of helping behaviour that may have been affected by social desirability and leaves many potentially confounding variables uncontrolled.

A number of studies have attempted to test the significance of kinship and Hamilton's rule using classic social psychology vignette or questionnaire designs (Burnstein, Crandall, & Kitayama, 1994; Kruger, 2003; Park & Schaller, 2005; Webster, 2004). In a series of hypothetical scenarios in which participants reported the likelihood

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of helping an individual as a function of genetic relatedness (with costs ranging from trivial courtesies to life-and-death heroic deeds), college students were more inclined to help relatives than non-relatives, and particularly so in life-and-death situations (Burnstein *et al.*, 1994; Korchmaros & Kenny, 2001; Kruger, 2003). While providing *prima facie* evidence in support of Hamilton's rule, these experimental paradigms are open to question on grounds of both internal and ecological validity. One study (Park & Schaller, 2005), for example, failed to impose any kind of cost (actual or hypothetical); others failed to eliminate non-genetic benefits (e.g. social desirability) as confounding variables. As anthropologists and social psychologists have repeatedly discovered, humans commonly say one thing, but do something entirely different (e.g. Bliezner & Adams, 1992; Freeman, 1999; Wolf, 2001). Hence, none of these studies provides secure evidence on which to base a claim about the role of kin selection in actual human altruistic *behaviour*.

In this paper, we report a series of three experiments designed to test the hypothesis that, when all else is equal, an individual's willingness to bear a genuine cost (physical pain) to the benefit of another is a function of the recipient's biological relatedness. Clearly, it would be improper to influence the reproductive success of either our participants or their relations to any significant degree. However, we believe that compelling evidence for altruism of this form can only be demonstrated under controlled conditions in which the costs to the participant and benefits to their recipients are in both cases real and measurable (as is conventional in studies of altruism in animals). While these may not be sufficient to affect reproductive success, the fact that the costs and benefits are not merely hypothetical can be used to test the prediction that altruistic behaviour is mediated by Hamilton's rule. We do not seek to contrast preferences for kin with other explanations for altruism, such as prosociality or reciprocity, whether direct (e.g. Trivers, 1971) or indirect (e.g. Alexander, 1987). Our aim is to assess the strength of the kinship effect so as to provide a firm background against which the role of other modulating influences can be assessed. As such, this is the first attempt to assess *experimentally* the impact of kinship on altruistic *behaviour*, rather than on declared inclinations.

In addition, we consider two further issues. First, kinship has significant culture-specific overtones (Keesing, 1975), which makes it important to assess the extent to which kin-biased altruism might be a culture-specific phenomenon. For instance, there is wide cross-cultural variation in kinship classification systems: social relatedness, as defined linguistically and culturally, often differs from biological relatedness (Jones, 2000; Sahlins, 1977), thereby failing to provide a reliable genealogical guide. In some terminologies, unrelated individuals may be classified as kin, while in others collateral relatives are assigned to the same kin category as much closer genetic kin (e.g. a father's brother's sons are classified as brothers: Jones, 2000); furthermore, some kinship classification systems (e.g. that of the South African Zulu; Gluckman, 1950) distinguish between kin of similar genealogical distance (a mother's and a father's sister), while others (e.g. English) do not. Such inconsistencies between biological and social kinship, and associated norms of behaviour risk confounding tests of genetic kinship and nepotism. We therefore conducted the experiments in two very different cultural environments (a UK student and a South African Zulu population) and asked whether the same patterns occurred despite these cultural differences.

Second, since reciprocity is an important basis for altruistic behaviour, we attempted to control for its likely impact in two separate ways: in one experiment, we included an unrelated best friend of the same sex as a prospective exchange partner ($r = 0$) as well

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as a children's charity ($r = 0$, but no potential for future exchange). In another experiment, participants specified, for each recipient of their altruism, whether they had received help from them in the past or expected to do so in the future.

Overview of experiments

All the experiments followed the same basic repeated measures design. Participants were asked to impose a cost upon themselves in the form of pain from a physical exercise in return for a proportionate material reward given to an individual or organization, whose identity was disclosed to the participant in advance of carrying out the exercise. The exercise was a standard isometric ski-training exercise (sitting as though on a chair with the back against a wall, with the calves and thighs at right angles to each other; Cabanac, 1986). Participants were asked to hold this position for as long as possible. The position becomes increasingly painful with time, because the weight of the trunk is born by the thigh muscles acting at right angles to gravity. The pain incurred does not bear a linear relationship to the duration for which the position is held: after approximately 100 seconds, it increases massively. The duration for which the participant held the position was recorded from the moment the position was adopted until the participant stood up or sat down on the floor. In the UK, this duration was measured via an infrared light-beam (mounted on two laboratory stands 45 centimetres from the ground) that passed beneath the participants' buttocks/thighs when the correct position was adopted. A computer connected to the infrared cells recorded the times between onset and offset of the beam. A lack of electricity at the South African sites prevented the use of electronic apparatus. Instead, the apparatus consisted of a nylon tripwire mounted 45 centimetres from the ground on a metal frame; duration was recorded on a stopwatch. Participants were advised that they could cease holding the posture at any time.

The length of time a participant maintained the position on a given trial was transformed into a material benefit for a recipient, who varied in biological relatedness to the participant (the coefficient of relationship, r, the independent variable). Each participant repeated the experiment with the recipient varied systematically between four principal categories: the participant ($r = 1$), a sibling or parent ($r = .5$), a grandparent, aunt, uncle, niece or nephew ($r = .25$), a cousin ($r = .125$). Before the experiment, each participant drew up a list of individuals for the three categories of genetic relatedness. Care was taken to ensure that only biological kin were included.

For each experiment, the relatedness category for the recipient of the payout was randomized across trials (using Latin squares). Before each trial, participants were told that the proceeds would be sent directly to a nominated individual, chosen at random by the experimenter from among those listed by the participant. Recipients were limited to individuals who were of reproductive age (16–45 years) and not cohabiting with the participant.

At the end of each trial, the duration for which the position was held was determined, and the fee appropriate to this calculated. Where the participant was the beneficiary, this was paid directly to them; otherwise, a cheque for the appropriate fee was sent to the nominated beneficiary along with a note explaining the origins of the donation. In South Africa, we used cash equivalents.

Participants were not informed of the time elapsed until a trial had been completed, or told the purpose of the experiment until after they had completed the full series of trials. The design of the project was formally approved by the University College London

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and University College Hospital Committee on the Ethics of Human Research. Participants were treated in accordance with the 'Ethical Principles of Psychologists and Code of Conduct' (APA, 1992) and the 'Code of Conduct, Ethical Principles and Guidelines' (BPS, 2000).

If participants follow Hamilton's rule, investment (time for which the position was held) should increase with the recipient's relatedness to the participant. In effect, we tested whether investment flows differentially down channels of relatedness.

EXPERIMENT 1

In this experiment, we tested the central prediction that willingness to invest altruistically declines as relatedness declines. We controlled for two possible confounding variables: participant gender and trial order.

Method

Participants

Participants were recruited from the student population at the University of Oxford. Participants completed a health questionnaire, and were excluded if they were older than 40, married or declared a medical condition. Sample sizes were 11 males and 13 females.

Procedure

Participants attended on successive days and carried out the experiment for one of the nominated categories of relatedness on each day. Participants received £0.40 per 20 seconds for which the posture was held, in addition to a flat rate fee of £1.00 for attending each trial. At the end of each trial, participants rated how much the recipient would value the receipt of money (in terms of their personal wealth relative to that of the participant, on a scale of 1–5, with a score of 3 = same as participant: *welfare value*).

Results

The length of time (in seconds) that male and female participants maintained the posture for is shown in Figure 1 as a function of the relatedness of the recipients.

The data were normalized by $\log_e$ transformations and entered into a 2×4 split-plot ANOVA with gender (male vs. female) as a between-subjects factor and recipient (degree of relatedness) as a within-subjects factor. There was no effect of gender ($F(1, 21) = 0.14$, $MSE = 0.82$, $p = .71$, $\eta_p^2 < .01$), indicating that males and females maintained the posture for similar periods.

There was a main effect of recipient ($F(3, 63) = 8.34$, $MSE = 0.06$, $p < .01$, $\eta_p^2 = .28$, all p values relating to tests of the directionality Hamilton's rule's predictions about kinship effects are one-tailed, all others are two-tailed). The interaction failed to reach significance ($F(3, 63) = 2.11$, $MSE = 0.06$, $p = .06$, $\eta_p^2 = .09$). In line with self-reports that university students are more inclined to help kin with whom they feel emotionally close (Korchmaros & Kenny, 2001) we ranked charity as less closely related than friend and found a reliable linear trend for recipient ($F(1, 21) = 18.55$, $MSE = 0.07$, $p < .01$, $\eta_p^2 = .47$), showing that the cost that participants imposed on themselves was proportional to the degree of relatedness of the recipients.

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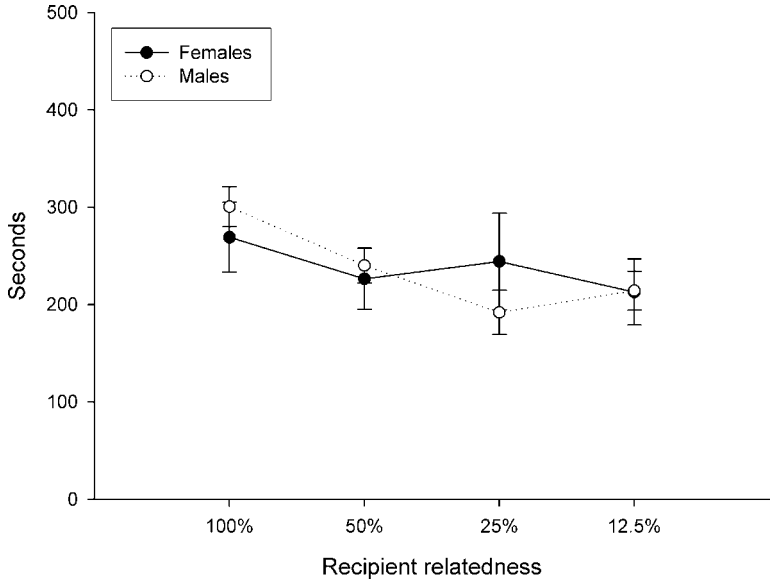


Figure 1. Experiment 1: Mean (± one *SE*) duration for which participants held a painful isometric skiing exercise as a function of the relatedness category of the recipient of the money that participants earned from doing so.

To examine the linear trend further, we conducted planned contrasts to compare differences in duration for each consecutive level of recipient. In line with convention, we used the pooled error term to control for Type 1 errors. Participants imposed a higher cost when the recipient was themselves ($r = 1$) than $r = .50$ ($F(1, 63) = 9.68$, $MSE = 0.06$, $p < .01$) and when the recipient was a $r = .50$ than $r = .25$ ($F(1, 63) = 3.38$, $MSE = 0.06$, $p < .05$). There was no difference in duration between $r = .25$ and $r = .125$ ($F < 1.0$).

Although the interaction between recipient and gender did not reach significance we examined each comparison separately for male and female participants. Males imposed a higher cost on themselves than $r = .50$ ($F(1, 63) = 11.52$, $MSE = 0.06$, $p < .01$); there was also a reliable difference between $r = .50$ and $r = .25$ ($F(1, 63) = 15.68$, $MSE = 0.06$, $p < .01$), and surprisingly males invested more in $r = .125$ than $r = .25$ ($F(1, 63) = 6.48$, $MSE = 0.06$, $p < .05$). While female participants imposed a higher cost on themselves than $r = .50$ ($F(1, 63) = 6.48$, $MSE = 0.06$, $p < .05$), they showed no difference between either $r = .50$ and $r = .25$ ($F < 1.0$) or $r = .25$ vs. $r = .125$ ($F(1, 63) = 2.00$, $MSE = 0.06$, $p > .05$).

Discussion

This experiment demonstrated that, in line with our prediction, there was a significant and reliable linear trend between the effort invested in the task (indexed as the duration for which the position was held) and the relatedness of the beneficiary (i.e. participants differentially favoured more closely related individuals). Although there were significant differences between successive categories of recipient, that between the two least related categories ($r = .25$ and $r = .125$) was, however, not itself significant. This might be because our behavioural measure is not sufficiently sensitive to pick up the finer

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differences in relatedness, or because other social variables (such as reciprocity) become more important than biological relatedness *per se*. There was some suggestion of a gender difference, with females acting more equitably across the relatedness categories than males, but the modest sample size makes it difficult to be certain that the absence of a significant difference between the two genders is not simply a consequence of greater variance in the women's data. This might be due to one of three possible reasons: (1) women exhibited greater variance than men, which might reduce the slope of the correlation for women; (2) women may discriminate on more dimensions (e.g. friendship and time spent together, as well as kinship) than men do, and hence their results may be less clear-cut when analysed against a single independent variable; and (3) the gender difference may be real: women may discriminate less in relation to relatedness than men do. In Experiment 2, we sought to control for these effects to explore gender differences more explicitly.

We may note four other possible sources of confound that might explain the observed results. First, if participants favoured themselves but did not discriminate between other individuals, this might create a significant albeit spurious positive relationship between relatedness and duration. Second, evolutionary theory does not consider relatedness as the only criterion for investment under Hamilton's rule. Since the central issue is *maximizing* the number of copies of a gene propagated into future generations, the age of the beneficiary is a critical consideration: older individuals inevitably produce fewer future offspring than younger ones and therefore have a lower *reproductive value* (Fisher, 1930), making them of potentially less interest for altruistic investment (for reviews, see Barrett, Dunbar, & Lycett, 2002; Hughes, 1988). The presence of both parents and siblings in relatedness category $r = .5$, and grandparents as well as aunts/uncles in relatedness category $r = .25$, could have the effect of progressively reducing the average performance if participants acted solely in terms of the recipients' reproductive value. The third possible confound is that reciprocity, rather than kinship, might explain the results, as reciprocity is an important factor regulating human relationships. Reciprocity might also explain the gender difference if one sex (men) acts in response to kinship, but the other (women) places greater weight on reciprocity. Fourth, recipient gender might play a significant role if disproportionately more males acted as recipients in trials with less closely related recipients: for instance men might behave more generously towards women than towards other men, either because of social norms or because they were showing off (a form of sexual display: Hawkes, 1991).

EXPERIMENT 2

In order to examine further the apparent gender difference and the possible sources of confounds identified above, we ran a second experiment with an increased sample size for both genders while controlling for reproductive value, reciprocity and recipient gender to remove some of the potential confounds in Experiment 1.

Method

Participants

Participants were 20 male and 20 female students from the University of London. All were healthy, single volunteers aged under 30 years (mean = 20.8, $SD = 2.7$ years). Of

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the participants 66% described themselves as British, 15% as North American, 5% as European and 12% as Asian.

Procedure

The procedure was as in Experiment 1, except that two additional trials with unrelated recipients were included: a same-sex best friend and a national UK children's charity. In addition, recipients were differentiated by kinship category (grandmother vs. aunt, parent vs. sibling) as well as by relatedness ($r = .25$ or $r = .5$).

Participants were rewarded with £0.70 per 20 seconds for which the posture was held, in addition to a flat rate fee of £1.00 for attending each trial.

Results

The mean length of time in seconds that participants maintained the posture for each level of recipient are shown in Figure 2. Following normalization by $\log_e$ transformation, these data were entered into a 2 × 6 split-plot ANOVA with gender as the between-subjects factor and recipient as the within-subjects factor. There was no main effect of gender ($F(1, 38) < 1.0$). There was a main effect of recipient ($F(5, 190) = 10.52$, $MSE = 0.05$, $p < .01$, $\eta_p^2 = .22$). The interaction between the two failed to reach significance ($F(5, 190) = 1.76$, $MSE = 0.05$, $p = .12$, $\eta_p^2 = .04$). As in Experiment 1 and consistent with our hypothesis, the linear trend of recipient was reliable ($F(1, 38) = 31.27$, $MSE = 0.06$, $p < .01$, $\eta_p^2 = .45$).

Planned contrasts revealed no reliable difference between $r = 1$ and $r = .50$ ($F(1, 190) = 1.54$, $MSE = 0.05$, $p > .05$). There was a reliable difference between

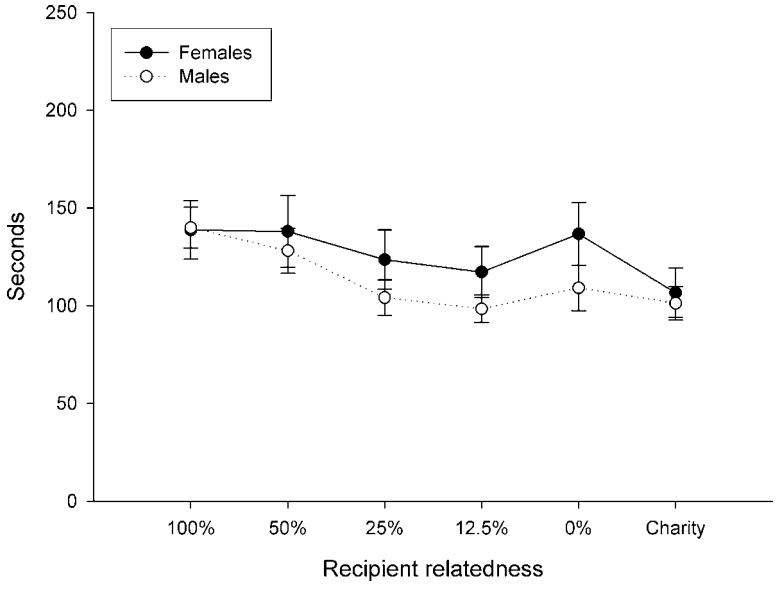


Figure 2. Experiment 2: Mean (± one *SE*) duration for which participants held a painful isometric skiing exercise as a function of the relatedness category of the recipient of the money that participants earned from doing so.

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$r = .50$ and $r = .25$ ($F(1, 190) = 6.14$, $MSE = 0.05$, $p < .01$), but no difference between $r = .25$ and $r = .125$ ($F < 1.0$). Participants were no more willing to invest in their best-friend than $r = .125$ ($F(1, 190) = 1.94$, $MSE = 0.05$, $p > .05$), but did invest more in their best-friend than charity ($F(1, 190) = 4.06$, $MSE = 0.05$, $p < .05$).

As in Experiment 1, we considered differences between males and females. Males invested more in themselves than $r = .50$ ($F(1, 190) = 2.40$, $MSE = 0.05$, $p < .05$, one-tailed), and more in $r = .50$ than $r = .25$ ($F(1, 190) = 10.58$, $MSE = 0.05$, $p < .01$). There were no reliable differences between $r = .25$ and $r = .125$ ($F < 1.0$), best-friend and $r = .125$ ($F < 1.0$), or best-friend and charity ($F < 1.0$). Females did not invest more in themselves than $r = .50$ ($F < 1.0$), although they favoured $r = .50$ more than $r = .25$ ($F(1, 190) = 2.90$, $MSE = 0.05$, $p < .05$, one-tailed). There was no difference between $r = .25$ and $r = .125$ ($F < 1.0$). Females however favoured their best-friend more than $r = .125$ ($F(1, 190) = 5.40$, $MSE = 0.05$, $p < .05$), and their best-friend more than charity ($F(1, 190) = 12.70$, $MSE = 0.05$, $p < .05$).

In Experiment 1, we identified three other sources of confound: reproductive value (some generations may be regarded as more worthy of altruistic investment than others), reciprocity (obligations based on a history of favours and exchanges) and recipient gender (in relation to normative behaviour or sexual display). Our concern is that one of these effects alone might explain the pattern of our results.

Two relatedness categories offer us the opportunity to test for the influence of reproductive value by comparing recipients of different generations ($r = .5$: parents vs. siblings; $r = .25$: grandparents vs. aunts/uncles). In each pairing, the first kinship category is older and therefore has a lower reproductive value. In neither case were there any significant differences in the duration for which the position was held (with duration $\log_e$-transformed: for $r = .5$, $F(1, 37) < 1$; for $r = .25$, $F(1, 38) = 2.45$, $p = .126$). Analysing the data separately for each sex of participant yielded similar results. Pooling of data from different generations can therefore be discounted as a possible explanation for our results.

The second potential confound was that reciprocal altruism might explain the main results. We tested this possibility in two ways: first, by including a best friend of the same gender and a children's charity, and second, less directly, by asking participants to assess the monetary value of the payout to the recipient on a five-point scale relative to how the recipient would value the money (*welfare value*). Overall, best friends fared as well as individuals related to the participant by $r = .25$, but not as well as the most closely related individuals (Figure 2; matched pairs, two-tailed binomial tests, $N = 40$: friends vs. $r = .5$, $p = .006$; friends vs. $r = .25$, $p = .134$). There was a striking gender difference: whereas both genders were less generous towards friends than relatives (more negative differences, albeit significant only in the case of men: $p = .012$), women treated best friends significantly better than they treated relatives of $r = .25$ (more positive differences: $p = .041$). When participants estimated the monetary value of rewards to the recipients, monetary value did not predict $\log_e$-transformed duration (males, $F(4, 75) = 1.37$, $p = .253$; females, $F(4, 175) = 0.97$, *ns*, with recipient categories self and charity excluded). Thus, while there seems to be some effect due to reciprocity, this was not sufficient to obscure the effects of kinship.

Friends received an average of 15.4% more investment than the other unrelated recipient category, charity (matched pairs, binomial test: $p < .001$). To check whether participants' involvement with or attitudes towards the charity to which they were being asked to make donations might affect their performance on charity trials, each participant was asked to state (a) whether they had been involved in any way with the

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specific charity and (b) their emotional approval for the work of the charity (on a −100/+100 analogue scale) before they started the experiment. On trials in which charity was the recipient, there was no significant difference in duration between participants who had and those who had not been involved with the charity over the previous 12 months (ANOVA with participant gender as a covariate: $F(1, 37) = 0.001$, *ns*). Similarly, degree of emotional approval for the work of the charity did not correlate with duration on charity trials ($r_s = -.039$, $N = 40$, $p = .813$). Analysing the two genders separately yielded similar results (females: $r_s = 0.242$, $N = 20$, $p = .305$; $r_s = -0.318$, $N = 20$, $p = .171$), although there was a strong suggestion of a gender difference ($t(38) = 3.641$, $p < .001$) with females being more positively disposed when they had an emotional commitment to the work of the charity. These findings indicate that this source of confound could not explain our main results with respect to kinship.

The third possible confound was a gender difference in favouring one *recipient* gender. With $\log_e$-transformed duration as the dependent variable, there was no effect due to either recipient gender ($F(1, 116) = 2.61$, $p = .109$) or the interaction between participant gender and recipient gender ($F(1, 116) = 2.03$, $p = .157$, with recipient categories self [$r = 1$] and charity [$r = 0$] excluded). Limiting the analyses to relatedness categories $r = .25$ and $r = .125$ (potential mates) yielded significant results for recipient gender in the case of females (males: $F(1, 78) = 0.14$, *ns*; females, $F(1, 78) = 3.95$, $p = .026$). Note, however, that this marginally significant result was due to female participants favouring *female* rather than male recipients (means of 138.1 vs. 105.8 seconds, respectively). This reinforces the finding that female participants differentially favoured the category same-sex best friend (Figure 2), but runs counter to the prediction based on potential mates tested here.

Discussion

The results confirm that there is a significant linear trend between effort invested and the relatedness of beneficiary, thereby confirming the basic pattern of kin-directed altruism observed in Experiment 1. They also verify that the results are not due to confounds from reproductive value, reciprocal altruism or recipient gender. As in Experiment 1, only some of the planned comparisons between successive degrees of relatedness are significant. Once again, the least reliable differences were most often those between the lowest degrees of relatedness. While friendship plays a significant role (especially for women), this effect does not completely obscure the influence of kinship. The charity category did not fare well; conceptualized beneficiaries (unidentified impersonal groups of people) do not attract significant investment, even when the groups targeted are particularly likely to attract empathy (e.g. children in need). Comparing investment in friend and charity (both unrelated recipients, but the former provides a potential for future exchange) suggests that the opportunity for reciprocation provides an advantage of approximately 15%. While this experiment confirms that there is neither a gender effect nor a gender/relatedness interaction, nonetheless these results confirm our suspicion that women do act more equitably towards individuals of differing relatedness.

One issue remains unclear. Given that there are significant cross-cultural differences in responses in micro-economic experiments (Henrich *et al.*, 2005), the question of whether the kinship effect is universal across human cultures or a peculiarity of the post-industrial European cultural environment needs to be assessed.

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EXPERIMENT 3

In order to determine whether non-European cultures exhibit effects similar to those found in Experiments 1 and 2, we replicated the experiment with two contrasting South African Zulu populations. These populations were both economically impoverished, but differed in the extent to which they were embedded in the modern economy. To focus on the core effects, we limited the study to males, as these had shown the strongest effects in Experiments 1 and 2. To ensure that the results were directly comparable to those of Experiments 1 and 2, we also ran Experiment 3 on a London population. Since the experiment was run at three separate sites, we identify the London study as 3a, and the two South African Zulu studies as 3b (Emmaus) and 3c (Hluhluwe).

Method

Participants

Experiment 3a used a sample drawn from a similar population as Experiment 2. Participants were 22 healthy, unmarried male volunteers, recruited from the University College London student community. The mean age was 22.5 years ($SD = 3.20$, range = 19–30). Seventy-three percent of the participants were single, the others described themselves as 'attached'. None had any children. Nineteen (86%) described themselves as British, two as Irish and one as South African.

The site for Experiment 3b was at Emmaus, a rural location in a remote valley in the Drakensberg Mountains. The site for Experiment 3c was the village of Hluhluwe, approximately 200 kilometres east of Emmaus; while still rural, this site is close to the main trade route between South Africa and Mozambique, and benefits economically and culturally from the road traffic. Both communities are characterized by extreme poverty and subsistence farming centred around traditional extended family homesteads and agnatic inheritance (Kruger, 2001). The adult population is female-biased due to high levels of male economic migrancy, resulting in discordance between traditional patriarchal norms and current functionally female-headed families. While a combination of financial hardship and high bridewealth effectively enforce marital monogamy, polygamy and high levels of infidelity in both traditional (Radcliffe-Brown & Forde, 1960) and contemporary (Lurie, Harrison, Wilkinson, & Karim, 1997) Zulu communities, along with limited availability of contraceptives, reduce the probability and confidence of relatedness. Both sites had a high HIV prevalence (Emmaus: 26.9%: Colvin & Gouws, 1999; Hluhluwe: 41.2%: Karim & Karim, 1999), yet to the best of the participants' knowledge all recipients were in good health.

In the South African studies, participants ($N = 31$ and $N = 20$, for Experiments 3b and 3c, respectively) were male volunteers selected from the local community according to the same criteria as in Experiment 3a. Participants ranged in age from 18–34 years, with mean ages of 22.1 ($SD = 4.97$) and 22.5 ($SD = 3.68$) years for Experiments 3b and 3c, respectively. All were South Africans who described themselves as ethnically Zulu. At both sites, approximately 95% of participants received no formal wage income; 75% described themselves as farmers and 25% as high school students. At Emmaus, 29% were single (58% childless), while at Hluhluwe 50% were single (90% childless).

Procedure

Participants attended on one day, and carried out the five conditions with a minimum of 15 minutes rest between trials. Participants performed the experiment for the same

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recipient categories as in Experiment 2 (except the category 'unrelated friend', which was excluded to avoid confounding the results through reciprocal altruism).

To avoid complications associated with reproductive value, all recipients were of reproductive age (mean age: London, 30.4 ± 12.0 years; Emmaus, 26.5 ± 8.0 years; Hluhluwe, 24.0 ± 8.7 years). In the South African sample, all recipients lived within 11 kilometres of the participant. Every effort was made to ensure that participants and recipients did not cohabit. Several of the Zulu participants (9 and 3%, respectively) lived in the same homestead, but none 'shared the same pot' (i.e. cooked communally with the participant). In experiments with the Zulu populations, diagrams were employed to preclude complications produced by different kinship classifications so as to ensure that, to the best of participants' knowledge, only full blood genetic relatives were included.

The experiments in London were carried out in the Psychology laboratory at University College London. In South Africa, they were carried out in local school buildings.

For Experiment 3, participants were not paid a flat rate fee for attendance, but received a payment at a rate of £1.50 per 20 seconds for which the position was held. For security and ethical reasons, the payments for the Zulu participants consisted of food hampers (containing six items considered desirable by local informants: oil, sugar, soya protein, tinned fish, instant soup and matches) of the same monetary value as in Experiment 3a (£1.50, equivalent to approximately ZAR20.00). Participants who maintained the exercise for 20 second received one hamper, while for 40 second they received two hampers, etc. The charity (a local school, around which much of the village life centred) received a cheque.

Apparatus and materials

Participants were asked to rate the welfare value of the donation to the recipient (relative to that of the participant: −10/+10), the frequency, importance and most recent date of previously received aid from the recipient (financial and social), expectancy of future financial aid and social support from the recipient, and the perceived pain from the exercise (0/+10). The questionnaire was translated into Zulu by two local Zulu assistants (assisted by Dr M. Bydawell of the University of Natal, who is fluent in both English and the regional Zulu dialect), and independently verified by a third assistant at each site to ensure accuracy and compensate for variations in dialect and connotative word meaning. The questionnaire was read to participants by a Zulu assistant.

Results

The results of Experiment 3 for each sample group are shown in Figure 3. The $\log_e$-transformed data were entered into three separate ANOVAs with recipient as a within-subject factor.

London

There was a reliable main effect of recipient ($F(4, 84) = 15.15$, $MSE = 0.07$, $p < .01$, $\eta_p^2 = .42$), and a reliable linear trend ($F(1, 21) = 49.80$, $MSE = 0.05$, $p < .01$, $\eta_p^2 = .70$). Planned contrasts revealed that participants were more willing to invest in

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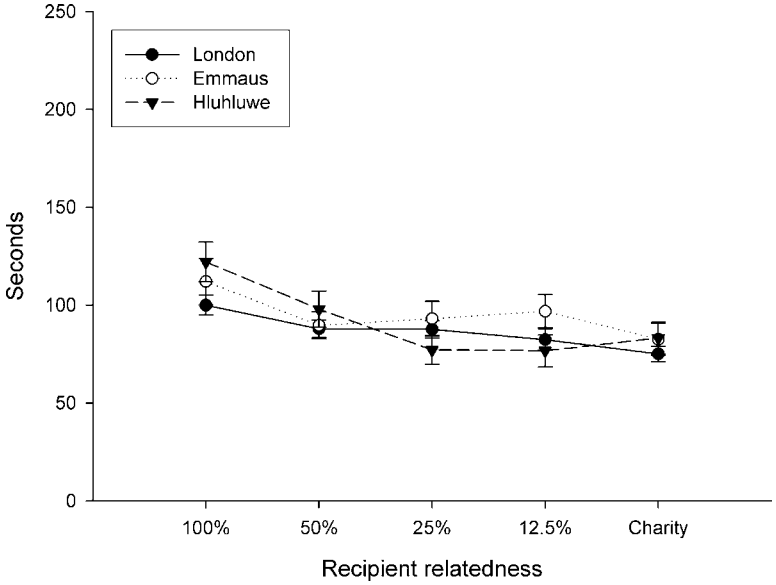


Figure 3. Experiment 3: Mean (± one *SE*) duration for which participants held a painful isometric skiing exercise as a function of the relatedness category of the recipient of the money that participants earned from doing so.

themselves ($r = 1$) than $r = .50$ ($F(1, 17) = 9.47, MSE = 0.07, p < .01$), and more willing to invest in $r = .50$ than $r = .25$ ($F(1, 17) = 9.87, MSE = 0.07, p < .01$). However, there were no reliable differences between $r = .25$ and $r = .125$ ($F < 1.0$), and $r = .125$ vs. charity ($F(1, 17) = 1.71, MSE = 0.07, p > .05$).

Emmaus

There was a reliable main effect of recipient ($F(4, 92) = 4.36$, $MSE = 0.05$, $p < .01$, $\eta_p^2 = .16$), and a reliable linear trend ($F(1, 23) = 13.69$, $MSE = 0.06$, $p < .01$, $\eta_p^2 = .37$). Planned contrasts revealed a significant difference between $r = 1$ and $r = .50$ ($F(1, 23) = 1.94$, $MSE = 0.05$, $p < .05$), but not between $r = .50$ and $r = .25$ ($F < 1.0$). Participants incurred a higher cost when the recipient was $r = .25$ vs. $r = .125$ ($F(1, 23) = 1.54$, $MSE = 0.05$, $p < .05$), and when $r = .125$ vs. charity ($F(1, 23) = 2.40, MSE = 0.05, p < .05$). (Some participants in the Emmaus and Hluhluwe samples did not have relatives of a reproductive age (16–45 years) in all categories: planned comparisons compare only the subset of 23 and 18 participants, respectively, that did.)

Hluhluwe

There was a reliable main effect of recipient ($F(4, 68) = 5.13$, $MSE = 0.06$, $p < .01$, $\eta_p^2 = .23$), and a reliable linear trend ($F(1, 17) = 11.67, MSE = 0.06, p < .01, \eta_p^2 = .41$). Planned contrasts revealed a reliable difference between $r = 1$ vs. $r = .50$ ($F(1, 68) = 8.00$, $MSE = 0.06$, $p < .01$), but no difference between $r = .50$ vs. $r = .25$ ($F < 1.0$), or between $r = .25$ vs. $r = .125$ ($F(1, 68) = 1.62$, $MSE = 0.06$, $p > .05$). However, participants were willing to invest more in their cousins ($r = .125$) than charity ($F(1, 68) = 9.68$, $MSE = 0.06$, $p < .01$).

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As in Experiment 2, two possible sources of confound were assessed: (1) recipient gender (males may be more willing to behave altruistically towards potential mates) and (2) reciprocity relationships.

With $\log_e$-transformed duration as the dependent variable, there was no effect due to recipient gender (Experiment 3a: $F(1, 80) = 0.55$, *ns*; Experiments 3b and 3c, pooled data sets: $F(1, 192) = 2.27$, $p = .134$; with recipient categories self [$r = 1$] and charity [$r = 0$] excluded). Limiting the analyses to relatedness categories $r = .25$ and $r = .125$ (potential mates) yielded even less significant results in respect of recipient gender (Experiment 3a: $F(1, 40) = 0.03$, *ns*; Experiment 3b + c: $F(1, 95) = 0.002$, *ns*).

We tested for the effects of reciprocal altruism by asking participants whether they had received financial or social (social or emotional) aid from the recipient in the past (yes/no) or expected such aid in the future (yes/no). Neither of the variables for past aid had a significant effect on $\log_e$-transformed duration (Experiment 3a: $F(1, 63) = 0.35$, *ns* and $F(1, 63) = 0.11$, *ns*, respectively; Experiment 3b + c, pooled data sets: $F(1, 141) = 0.34$, *ns* and $F(1, 94) = 0.01$, *ns*; with recipient relatedness as a covariate, and recipient categories self and charity excluded); similarly, with the exception of past help for the London sample, neither expectation of future financial help nor expectation of future non-financial help significantly affected task duration (Experiment 3a: $F(1, 63) = 6.01$, $p = .017$ and $F(1, 63) = 1.50$, *ns*, respectively; Experiment 3b + c, pooled data sets: $F(1, 94) = 0.03$, *ns* and $F(1, 94) = 0.05$, *ns*, respectively).

Finally, neither involvement with the charity (ANOVA, with gender and recipient relatedness as covariates: $F(1, 37) = 0.66$, *ns*) nor attitude towards the charity ($r^2 = .016$, $df = 38$, $p = .212$) significantly influenced the duration for which the position was held, and thus did not explain the poor performance on the charity trials.

Discussion

These results replicate the findings from Experiments 1 and 2: participants modulated the effort they were prepared to expend as a function of recipient relatedness, and did so, broadly, as a decreasing function of relatedness. Once again, a number of the planned contrasts (and particularly those between the more remote categories of relatedness) were not individually significant. Reciprocity and recipient gender can again be excluded as likely explanations for the main results. Experiment 3a confirmed that the slight variation in experimental design did not produce a different pattern of results from those previously obtained in Experiments 1 and 2. The results confirm that the effect of kinship is trans-cultural, and not affected by differences in experimental design (including the mode of payment). In other words, Hamilton's rule is not limited to the peculiar cultural environment now characteristic of the post-industrialized West.

Two features of the results however do suggest a cross-cultural difference, albeit overlaid on a general pattern. First, the two South African societies, although not the London participants, discriminated between $r = 0.125$ and $r = 0$. Second, in contrast to the London sample, there was in the two South African societies no discrimination between investment in kin with $r = 0.5$ and 0.25. The latter difference in patterns of investment may reflect that Zulus live in extended families and that such cohabitation and close association during the early stages of life may function as a proximate cue of relatedness among kin, in a manner similar to the way in which early childhood

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association activates adaptive kin-recognition responses among non-kin (e.g. Shepher, 1971; Westermarck 1891; Wolf, 1970, 1995).

GENERAL DISCUSSION

These results provide experimental evidence in support of the claim that humans titrate their willingness to incur costs for the direct benefit of others as a direct function of biological relatedness. As such, they provide the first compelling *experimental* evidence that humans abide by Hamilton's rule when making judgments about how to *behave* towards others. In contrast to all previous studies, the present design obliged participants to incur a significant genuine cost (pain, in contrast to a hypothetical risk or experimenter-donated money used in previous studies) when making these decisions, thereby meeting one of the crucial assumptions of the theory of kin selection. Although these costs and benefits may not of themselves significantly influence reproductive success, the pain experienced signals imminent tissue damage and can be considered a significant cost that, in an evolutionary context, would have a direct effect on fitness if avoidance action was not taken. The results thus show that actual human altruistic *behaviour* is mediated by Hamilton's rule. While other studies (e.g. Caporeal *et al.*, 1989) have found that altruistic and prosocial behaviour is widespread, our results demonstrate that the tendency to behave altruistically is sensitive to the costs involved, as predicted by Hamilton's rule, thereby emphasizing the crucial role that the costs of action have in the decision to behave altruistically.

Despite the consistency of the broad pattern of the results, however, some of the differences between successive categories of kinship were individually not significant. Most of these involved the more distal categories, which are also those with the smallest absolute differences in relatedness. This might reflect that our behavioural assay was too blunt to be able to pick up small differences, a conclusion that gains support from the fact that some of the more distal comparisons did yield significant differences. It might, however, equally reflect the fact that the relationship with relatedness is not strictly linear, perhaps because other factors (social familiarity, friendship, etc.) may cut across pure relatedness. The fact that charity (a category for which these effects would not apply) consistently did less well than friend and relatedness category $r = .125$ might be interpreted as support for this suggestion. Further work is needed to clarify this.

Irrespective of the *intentions* that motivate human behaviour, these results demonstrate that humans *behave* in such a way as to maximize inclusive fitness: they are more willing to benefit closer relatives than more distantly related individuals. Demonstrating the effect in two different cultures (including a population relatively isolated from mainstream contemporary Western economics and culture) suggests that this phenomenon has broad applicability beyond post-industrial European society. The results thus support the relevance of Hamilton's rule as a *functional* explanation for human behaviour. This however, does not tell us anything about the motivations that underpin the behaviour, or the cues that are used to infer relatedness.

By the same token, this does not mean that humans never behave altruistically towards others for reasons unrelated to biological kinship. There are several reasons other than kin selection as to why humans (and other animals) may behave altruistically: these include reciprocal altruism and mutualism (for a review, see Barrett *et al.*, 2002), as well as enforced moral or ethical obligations (whereby humans impose obligations on each other to force community members to behave altruistically in order to further long-term collective advantage through communal solidarity: Dunbar, Barrett, & Lycett,

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2005; Sober & Wilson, 1998; Fehr & Fischbacher, 2002). Our aim has been to use an experimental design to isolate one key component (biological kinship), so as to determine whether or not Hamilton's rule underpins any aspect of human behaviour.

These results demonstrate that Hamilton's rule provides a baseline against which humans make judgments that may be subsequently coloured by issues of reciprocity, obligation, prosociality and other ethical considerations. Having shown that Hamilton's rule applies, it is nonetheless unlikely that humans use genetic relatedness itself as the proximate basis for discriminating between individuals. We might anticipate that, similar to other animals (e.g. Hepper, 1986; Porter & Moore, 1981), humans use cues such as affection, cohabitation, or social norms as proxies for relatedness.

The difference between men and women merits further comment. The results of Experiments 1 and 2 suggest that, in deciding whether to behave altruistically, women may rely less on kinship cues than men do. One reason for this might be that humans are typically a female-dispersal species (Foley & Lee, 1989; Rodseth, Wrangham, Harrigan, & Smuts, 1991; Seielstad, Minch, & Cavalli-Sforza, 1998) in which males form patrilinearly related groups that exchange women (at least in traditional societies that are economically dependent on heritable wealth). One consequence is that, in traditional societies, women will inevitably spend most of their reproductive lives in groups where they have few genetic relatives (other than their own children).

This is likely to have two important consequences. One is to encourage women to be more attuned to maintaining close relationships with both kin and other unrelated but significant members of the community. Oates and Wilson (2002), for example, reported that, in a study of responses to unsolicited emails requesting help on a project, women were more likely than men to answer if they shared the same name(s) as the message sender (name-sharing being taken as a proxy for relatedness, as it is in many cultures). Similarly, Salmon (1999) found that women were more likely than men to keep contact with distant kin, while Eagley and Crowley (1986) reported that women (but not men) were more likely to help friends and close kin rather than strangers (see also Johnson, 1996). The second consequence might be for women to engage in a more equitable (and hence reciprocally based?) exchange of resources and services (or, alternatively, to titrate their altruism in response to a wider range of cues) within the community. In contrast, men have more opportunity to target their altruism towards a wide range of biological relatives. In this respect, female participants' willingness to invest heavily in same-sex best friends in Experiment 2 contrasts strikingly with a much reduced tendency to favour same-sex friends among males.

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Author Note

Trials using these methods were carried out and filmed in the course of making a BBC programme about this research, broadcast in 2002. These trials did not provide any of the data reported here.

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