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Altruism towards cousins

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Recent research on kin investment shows a matrilateral bias as a function of paternity uncertainty. Kin investment, however, is a special case of kin altruism. We thus hypothesize that psychological adaptations have evolved to regulate cousin-directed altruism according to predictably variable levels of paternity uncertainty in different categories of cousins. We develop a formal mathematical model that predicts that individuals should be most willing to act altruistically towards their mother's sister's (MoSis) children and least willing to act altruistically towards their father's brother's (FaBro) children. Altruism towards father's sister's (FaSis) and mother's brother's (MoBro) children are predicted to fall in between. An empirical study ($N=195$), assessing expressed altruistic proclivities, confirmed the predictions from the model. Participants expressed willingness-to-help following the descending order: (i) MoSis children, (ii) MoBro children, (iii) FaSis children, and (iv) FaBro children. The psychological variables of emotional closeness, empathic concern and contact frequency showed precisely the same pattern across distinct cousins, providing convergent confirmation of the model. The results support the hypothesis of cousin-specific adaptations sensitive to varying probabilities of paternity uncertainty.

Keywords: paternity uncertainty; kin altruism; cousin; psychological adaptation; kin selection

1. INTRODUCTION

Kin relationships are composed of many subunits, such as motherhood, fatherhood, grandparenthood and sibship. Evolutionary approaches suggest that qualitatively distinct kin relationships have posed recurrently different adaptive problems to human ancestors, resulting in relationship-specific psychological adaptations (Wilson & Daly 1997; Kurland & Gaulin 2005). The evolved psychologies of motherhood and fatherhood have been actively explored in recent decades (Geary 2005; Salmon 2005). The study of grandparents, uncles and aunts has received some attention (Euler & Weitzel 1996; Gaulin *et al.* 1997; Michalski & Shackelford 2005). Aside from the anthropological investigation of cousin marriages (Levi-Strauss 1969), the psychology of cousin relationships has remained entirely unexplored.

Owing to a key feature of mammalian, primate and human reproductive biology—internal female fertilization—paternity probability has proven to be a key predictor of paternal investment. Since women may cuckold their long-term mates through extra-pair copulations, males experience reduced paternity. Not all of men's putative offspring are their genetic offspring. As compromised paternity probability reduces the reproductive payoff of a male's investment, selection should favour reducing investment in response to reduced paternity (Trivers 1972; Houston & Davies 1985; Winkler 1987). In humans, considerable empirical evidence indicates that fathers do invest less in parental care as their paternity is reduced (Anderson *et al.* 1999; Marlowe 1999).

Reduced paternity has also been shown to affect the investment strategies of grandparents. Because the vertical links through males are less certain than the links through females, the number of uncertain links between distant family members theoretically should predict interactions with distant kin. For example, a maternal grandmother is connected to her grandchildren through two certain links; a maternal grandfather and a paternal grandmother are connected through one certain and one uncertain link; and a paternal grandfather is connected through two uncertain links. Smith (1988) predicted that maternal grandmothers should invest in their grandchildren the most, followed by both maternal grandfathers and paternal grandmothers, with paternal grandfathers investing the least. Empirical tests supported the prediction (DeKay 1995; Euler & Weitzel 1996; Pashos 2000; Laham *et al.* 2005; Michalski & Shackelford 2005). Matrilateral aunts and uncles are predicted to invest more in nieces and nephews than patrilateral aunts and uncles. The laterality and sex-of-investor biases have been documented (Gaulin *et al.* 1997; McBurney *et al.* 2002).

Because investment in kin of the next generation constitutes just one form of kin altruism, the logic of differential altruism as a function of differential paternity uncertainty should extend to investment patterns among cousins. Cousins come in four categories based on the relationship to the focal individual: mother's sister's (MoSis) children; mother's brother's (MoBro) children; father's sister's (FaSis) children; and father's brother's (FaBro) children. A focal individual can be completely 'certain' (no conscious awareness implied) that all putative MoSis children are genetically related to herself or himself by a coefficient of relatedness of one-eighth. One uncertainty link occurs for putative FaSis children and MoBro children. And two uncertainty links occur for putative FaBro children (figure 1; although there could be another uncertain genetic link between the focal individual's parent and her or his aunts/uncles, such uncertainty would be the same across each cousin categories and hence can be ignored for the present purposes). We therefore hypothesized that psychological adaptations

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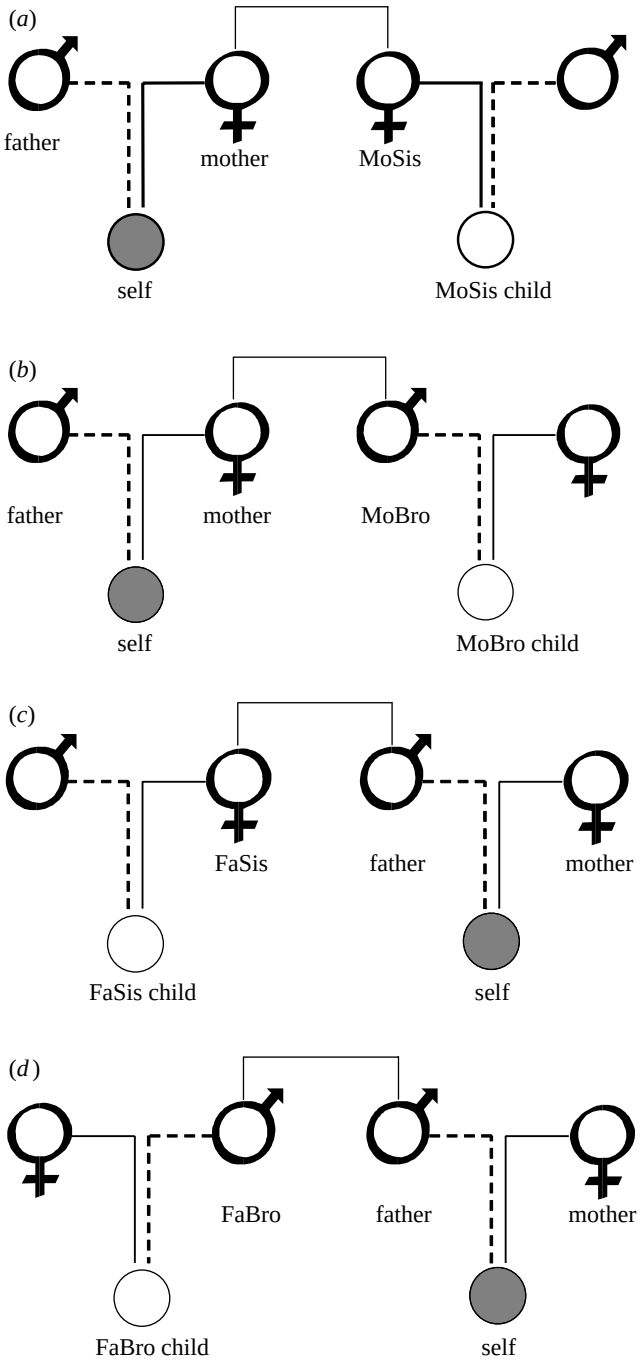

Figure 1. The genealogical links between self and different categories of cousins. (*a*) A self and its mother's sister's (MoSis) children. (*b*) A self and its mother's brother's (MoBro) children. (*c*) A self and its father's sister's (FaSis) children. (*d*) A self and its father's brother's (FaBro) children. The dashed line indicates that within-pair paternity might be reduced due to cuckoldry.

have evolved to regulate cousin-directed altruism in response to the varied levels of paternity uncertainty across the categories of cousins. We construct a kin selection model of altruism towards distinct cousins, showing that hypothesized evolved decision rules will lead one to act most altruistically towards one's MoSis children, followed by both FaSis children and MoBro children, and lastly FaBro children (see Appendix A).

Based on this formal model of discriminative cousin altruism, this paper presents empirical tests of the model's key prediction that willingness to act altruistically towards cousins will follow the order (i) MoSis children, (ii) both MoBro and FaSis children and (iii) FaBro children. We conducted a study that explored willingness to help cousins using hypothetical dilemmas involving life-and-death situations. Recent research has shown that psychological variables such as emotional closeness, empathic concern and the frequency of contact may mediate the effect of genetic relatedness on decisions to act altruistically towards kin (Korchmaros & Kenny 2001, 2006; Neyer & Lang 2003). We predicted that emotional closeness, empathic concern and the frequency of contact would also follow the same order across the distinct categories of cousins, affording three additional empirical tests of the model.

2. MATERIAL AND METHODS

(a) *Participants*

One hundred and ninety-five undergraduate students from the University of Texas at Austin (84 women and 111 men) participated in this study. We made clear in the recruiting stage that only those with one or more cousins would be eligible to participate. The mean age of participants was 19.8 ($\pm$s.d. 1.5) years (range = 18–27).

(b) *Investment instrument*

The first section of the instrument requested basic demographic information of participants (age, sex, ethnicity and socioeconomic status (SES)). We explicitly defined the four categories of cousins so that participants could clearly distinguish each cousin category (e.g. 'paternal aunt's children (i.e. FaSis children)'). Participants were asked to consider only their 'blood-related' cousins and to ignore any genetically unrelated cousins through step-parents or foster parents. For each cousin category, participants were instructed to think of the cousin whose age is closest to their own. This restriction was designed to prevent introducing any bias that might occur if participants chose their favourite cousin from each type of cousins. The demographic information (age, sex and SES) of each cousin was obtained. The remaining sections of the instrument were repeated for each category of cousins; hence, participants who had all the four categories of cousins answered four times for each question.

The second section assessed psychological variables hypothesized to mediate the association between genetic relatedness and kin-directed altruism: emotional closeness, empathic concern and the frequency of contact. Participants were evaluated, using a seven-point rating scale from 1 (not at all) to 7 (very much), on how emotionally close they felt to each cousin. Using the same seven-point scale, they also evaluated how much they cared for the well-being of each cousin. They were further evaluated, using a 10-point rating scale from 1 (never) to 10 (every day), on how often they communicated with each person by email, phone, letter or in person.

The third section measured the participants' willingness to act altruistically towards cousins in a hypothetical dilemma involving life-or-death situations. Participants read the following scenario:

As you make your way through the city you walk past a building that is blazing with flames. You instantly realize that the building has been housing a meeting attended by your cousin _____ (fill in the initials). Your cousin _____ in the rapidly burning building badly needs your help, yet entering the burning building to save him or her would risk injury to you.

Table 1. Forced-choice data of willingness-to-help scores and other psychological variables for the subsample having all four cousin categories ($N=56$). (The asterisk indicates significant differences ($p<0.001$).)

	willingness-to-help	emotional closeness	empathic concern
observed distribution (MoSis : MoBro : FaSis : FaBro)	26 : 3 : 14 : 13	27 : 10 : 8: 11	31 : 6 : 7 : 12
χ^2 of overall null hypothesis (MoSis : MoBro : FaSis : FaBro = 1 : 1 : 1 : 1)	19.0*	16.43*	29.0*
χ^2 of null hypothesis no. 1 (MoSis : MoBro + FaSis = 1 : 2)	14.24*	6.145*	27.28*
χ^2 of null hypothesis no. 2 (MoBro + FaSis : FaBro = 2 : 1)	1.35	0.277	2.42

Participants were asked on a seven-point rating scale from 1 (extremely unlikely) to 7 (extremely likely): 'how likely would you enter the burning building and attempt to save your cousin's life, despite the considerable harm to you?' Information about the residential distances between participants and each category of cousins was collected in order to examine whether residential distance acts as a confounding variable that could affect the willingness-to-help scores. The rating scale was based on the logarithmic 10-point scale developed by Euler & Weitzel (1996).

Finally, we asked forced-choice questions about emotional closeness, empathic concern and the willingness to help cousins. Participants were asked, for example, 'among those different kinds of cousins you actually have, which kind of cousin are you emotionally closest to?' Participants having only one category of cousin were instructed not to answer.

(c) *Dataset and statistical analysis*

Fifty-six participants had all four categories of cousins. Statistical analyses were performed for those 56 participants having all four categories of cousins and for all participants ($N=195$) having at least one category of cousin. The number of cousin categories the participants had did not affect the average rating of the willingness-to-help (one-way ANOVA, $F(3,194)=1.24$, n.s.). Although the willingness-to-help scores and other psychological variables were negatively skewed (skewness coefficient $=-1.00$), parametric statistics were used in this study because the F-statistic is quite robust to moderate violations of the normality assumption (Cohen 1969). We confirmed that both non-parametric tests and data transformation to handle non-normality produce nearly identical results.

3. RESULTS

There were no significant main effects or interactions for the sex of participant in responses on force-choice items or rating-scale items, nor were there any significant main effects or interactions for the sex of participants' cousins. Therefore, the data were collapsed across the two variables (sex of participants and sex of participants' cousins) in subsequent analyses.

(a) *Forced-choice life-or-death data*

The 56 participants who had all the four categories of cousins were asked which cousin they would help the most in a hypothetical life-or-death situation. The overall null hypothesis would dictate that each category of cousins would be equally chosen by chance alone. The observed distribution of choices was 26 : 3: 14 : 13 for MoSis children, MoBro children, FaSis children and FaBro children, respectively. A χ^2-test revealed that the observed distribution was significantly different from the distribution expected by chance, supporting the first prediction in this study ($\chi^2_3=19.0$, $p<0.001$). Next, we collapsed the MoBro children and FaSis children into a single composite and tested the null sub-hypothesis of 1 : 2 for the MoSis children and the composite. A significant difference was also detected ($\chi^2_1=14.24$, $p<0.001$). Lastly, we tested the null hypothesis of 2 : 1 for the composite variable above and the FaBro children. The χ^2-test failed to detect a significant difference ($\chi^2_1=1.35$, $p=0.245$). Therefore, our hypothesis that the order of willingness-to-help scores would be MoSis > MoBro = FaSis > FaBro was generally supported, except that FaBro children would be helped the least (table 1).

Similar results were obtained for the forced-choice items about emotional closeness and empathic concern. For both items, the overall null hypothesis that each category of cousins would be equally chosen was rejected. Further, the null sub-hypothesis of 1 : 2 for MoBro children and the composite variable noted above was rejected. The null sub-hypothesis of 2 : 1 for the composite variable and FaBro children, however, was not rejected (table 1).

(b) *Willingness to act altruistically, emotional closeness, empathic concern and the frequency of contact*

(i) *Willingness to act altruistically towards cousins*

Our prediction was that willingness to act altruistically towards cousins would be arranged in the following order: (i) MoSis children, (ii) both MoBro and FaSis children and (iii) FaBro children. We controlled the effects of the residential distance between participants and each of their cousins and the age difference between the two. Cousins who happened to live close to each other would have more opportunities to develop cooperative relationships than those living far away, so the residential distance may act as a confounding factor. Indeed, for the total sample of participants, repeated measures ANOVA revealed that the residential distance between participants and cousins was marginally significantly different across the four cousin categories ($F(3,355)=2.558$, $p=0.055$). Another potential confounding factor is age, since the age differences between participants and their cousins may affect cousin-directed altruism. For the total sample, the age difference between participants and cousins differed significantly across the four cousin categories ($F(3,355)=5.952$, $p=0.001$). Thus, our subsequent analysis included the residential distance and the age difference as covariates.

Repeated measures analysis of covariance (ANCOVA) with the two covariates was conducted on the

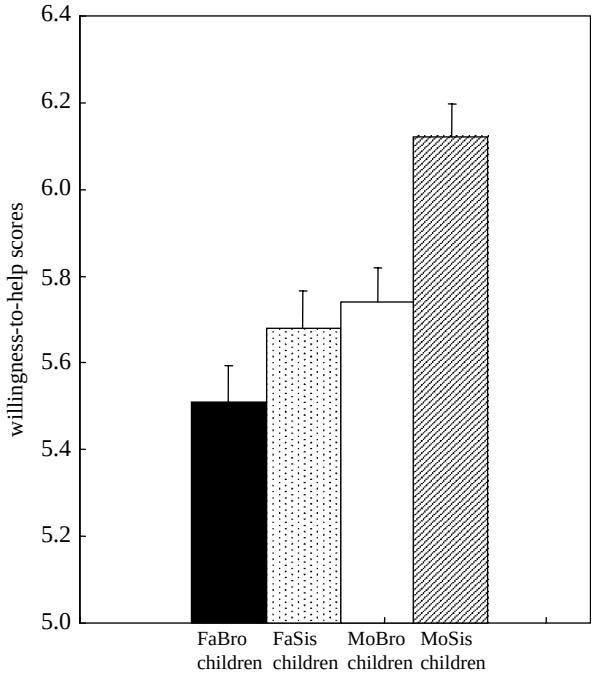

Figure 2. The adjusted mean ratings (and standard error) of willingness-to-help scores among four different cousin categories, controlling for age differences and residential distance.

willingness-to-help scores for the total sample of participants. There was a highly significant main effect of different cousin categories on the willingness-to-help scores ($F(3,352)=10.848$, $p<0.001$). The mean ratings were arranged in the following order: MoSis children, MoBro children, FaSis children and FaBro children (table 2). A significant linear trend was revealed ($F(1,352)=28.489$, $p<0.001$). The results confirm our first prediction that cousin-directed helping tendencies would be arranged in the order of (i) MoSis children, (ii) both MoBro and FaSis children and (iii) FaBro children. Planned repeated comparisons where adjacent group means are compared showed that participants were significantly more willing to help their MoSis children than their MoBro children ($p=0.001$), but not significantly more willing to help their MoBro children than their FaSis children ($p=0.616$). Participants were slightly more willing to help their FaSis children than their FaBro children, although this comparison did not reach statistical significance ($p=0.151$). Overall, the difference between the adjusted means of FaSis children and FaBro children was much greater than the difference between MoBro children and FaSis children (figure 2).

A similar analysis for the subset of participants having all the four categories found the same pattern. The effect of the different cousin categories on the willingness-to-help scores was significant (repeated measures ANCOVA, $F(3,163)=3.813$, $p=0.011$) and a significant linear trend was detected ($F(1,163)=10.60$, $p=0.001$). Owing to the reduced sample size, planned repeated comparisons revealed that only the difference between the adjusted ratings of MoSis children and MoBro children was marginally significant ($p=0.084$). Given that both the samples show the same pattern of ratings, we hereafter focus on the total sample, which had greater statistical power.

(ii) *Emotional closeness, empathic concern and the frequency of contact*

The ratings of three possible predictors of cousin-directed altruism were significantly correlated with one another ($r=0.59$ for emotional closeness and concern, $r=0.72$ for emotional closeness and contact and $r=0.45$ for concern and contact; all ps <0.01). These correlations provide circumstantial evidence for the reliability and validity of these variables as indices of altruism towards cousins. Indeed, each of the predictors was significantly correlated with the willingness-to-help scores ($r=0.44$ for empathic concern, $r=0.42$ for emotional closeness and $r=0.31$ for contact frequency; all ps <0.01).

To test the prediction that the three predictors should also be arranged in the order predicted by our model, a repeated measures ANCOVA including residential distance and age differences as covariates was conducted on each variable. Emotional closeness ratings were significantly different across distinct cousin categories ($F(3,352)=10.961$, $p<0.001$), showing a significant linear trend ($F(1,352)=28.13$, $p<0.001$) in which the adjusted mean ratings were arranged in the same way as willingness-to-help ratings (table 3). Planned repeated comparisons found that the difference between MoSis children and MoBro children was significant ($p=0.001$). Neither the difference between MoBro children and FaSis children nor between FaSis children and FaBro children was significant.

Analyses conducted on empathic concern ratings revealed a significant main effect of different cousin categories on empathic concern (repeated measures ANCOVA, $F(3,352)=5.548$, $p=0.001$), revealing a significant linear trend ($F(1,352)=10.367$, $p=0.001$). Consistent with the prediction, the adjusted mean ratings were arranged in the descending order of (i) MoSis children, (ii) FaSis children, (iii) MoBro children and (iv) FaBro children.

The ratings of contact frequency were also significantly different among different cousin categories (repeated measures ANCOVA, $F(3,352)=8.492$, $p<0.001$) and showed a significant linear trend ($F(1,352)=19.99$, $p=0.001$). The adjusted mean ratings were arranged in the same way as empathic concern. Participants were concerned about their MoSis children significantly more than their FaSis children ($p<0.001$), not significantly concerned about their FaSis children than their MoBro children ($p=0.851$) and not significantly concerned about their MoBro children than their FaBro children ($p=0.174$).

4. DISCUSSION

The current research investigated the hypothesis, derived from a formal mathematical model, that humans have relationship-specific psychological adaptations for cousin-directed altruism sensitive to the different levels of paternity uncertainty across categories of cousins. Based on the varied paternity probability, the model of altruism towards cousins predicted that MoSis children would be the most favoured, followed by both MoBro and FaSis children, with FaBro children coming out last. Participants reported a willingness to act altruistically towards their MoSis children the most, followed by their MoBro children, their FaSis children and lastly their FaBro children. These results strongly confirm the central

Table 2. Raw and (adjusted) mean ratings of willingness-to-help across distinct cousin categories, adjusted for age differences and residential distance.

	total sample ($N=195$)			those having all the four cousins ($N=56$)	
category of cousins	mean	s.d.	N	mean	s.d.
MoSis children	6.05 (6.12)	1.42	149	5.89 (5.88)	1.23
MoBro children	5.73 (5.74)	1.46	148	5.59 (5.58)	1.36
FaSis children	5.59 (5.68)	1.32	126	5.39 (5.42)	1.55
FaBro children	5.50 (5.51)	1.11	131	5.34 (5.34)	1.67

Table 3. Raw and (adjusted) mean ratings of emotional closeness, empathic concern and contact frequency across distinct cousin categories for the total samples of participants, adjusted for age differences and residential distance.

		emotional closeness		empathic concern		contact frequency	
category of cousins	N	mean	s.d.	mean	s.d.	mean	s.d.
MoSis children	149	4.70 (4.56)	1.61	5.69 (6.04)	1.47	5.25 (5.13)	2.35
MoBro children	148	3.91 (3.88)	1.65	6.02 (5.58)	1.22	4.33 (4.28)	2.24
FaSis children	126	3.57 (3.58)	1.96	5.53 (5.61)	1.54	4.16 (4.32)	2.17
FaBro children	131	3.66 (3.49)	1.90	5.51 (5.53)	1.57	4.00 (3.97)	1.99

prediction from the model. Moreover, the pattern of psychological predictors of kin-directed altruism—emotional closeness, empathic concern and contact frequency—across distinct cousin categories provided three additional confirmations of the model's predictions.

The present study failed to detect a statistically significant difference between altruism towards FaSis children and FaBro children. It is reasonable to conclude, however, that FaSis children are the least likely to be helped among all the four cousin categories, because (i) the mean rating of FaSis children was invariably the lowest in the willingness-to-help scores, as well as in all the three psychological variables affecting altruism, (ii) the predicted linear trends proved to be highly significant for all the four dependent measures, and (iii) FaSis children were helped more than FaBro children, as predicted, although it just missed conventional significance. Given that MoSis children were always ranked at the top position with a high statistical significance ($p \leq 0.001$) for all dependent measures, it remains to be revealed why the degree to which FaBro children are the least likely to be helped appears not to be as robust as expected.

Previous studies on the effect of paternity uncertainty on kin relationships have centred on the investment in putative kin of the next generations, notably paternal investment, grandparental investment and the investment of aunts and uncles (Geary 2005; Kurland & Gaulin 2005). To our knowledge, the present research is the first study to show that *differential altruism towards kin of the same generation* can also be predicted by varying levels of paternity probability. Whereas people apparently have the intuitive notion that reduced paternity results in reduced investment into the next-generation kin (e.g. as reflected in the folk saying 'Mama's baby, Papa's maybe'; Buss 2000), it remains to be clarified at the proximate level the precise mechanisms by which altruism towards different cousins is affected by variable levels of paternity uncertainty in the parental generation.

One hypothesis is that altruistic tendencies towards their cousins will be largely determined by the quality of adult sibling relationship linking two families in the parental generation (J. Woolley 2006, personal communication). Contact and affection between siblings in adulthood appears to be greater in sister–sister pairs than in mixed-sex pairs, with brother–brother pairs having the least contact and affection (White & Riedmann 1992). Thus, an individual may be willing to help the MoSis children the most because mothers have kept on good terms with each other as sister–sister dyads. The hypothesis is consistent with the previous findings that (i) matrilateral aunts and uncles invest more in their nephews and nieces than patrilateral aunts and uncles and (ii) aunts invest more than uncles regardless of laterality (Gaulin *et al.* 1997; McBurney *et al.* 2002). Indeed, the sister–sister adult dyads are most likely to invest in each other's children (i.e. in their nephews and nieces) due to the absence of reduced maternity from each sister's viewpoint, thus maintaining more cooperative relationships than other types of adult sibling dyads. This could represent one proximate path through which the predicted discriminative altruism towards cousins occurs. In short, evolved decision rules for cousin-directed altruism may have been designed to convert important environmental inputs, such as the quality of sibling relationships in the parental generation, into the cognitive or behavioural outputs for discriminative altruism towards cousins.

Other environmental inputs processed by psychological adaptations for cousin-directed altruism may include the age differences between cousins and the amount of contact early in life resulting from residential distance (the two variables that were treated as covariates in this study). The age differences and residential distance may reflect sex differences in age at marriage and dispersal, respectively (Euler & Weitzel 1996; Gaulin *et al.* 1997). Because men on average marry later in life than women do, it follows that (i) FaSis children will be older on average than one's own siblings, (ii) MoBro children will be younger on average than one's own siblings, and (iii) FaBro and MoSis children will be the same age on average. The mean age differences across distinct cousin categories in our study

were $(-1.34):(+1.18):(-1.87):(+0.37)$ for FaBro children : FaSis children : MoBro children : MoSis children, respectively, which roughly coincides with our inference. Because individuals should be more willing to help their cousins younger than themselves and less willing to help cousins older than themselves, altruism towards MoBro children may be augmented and altruism towards FaSis children reduced due to the age differences between a focal individual and each category of his or her cousins.

The current research is based on the assumption that the information gained from self-reports reliably reflects the actual altruistic behaviour towards kin. Previous studies of kin investment have shown that it does correspond well to the actual altruistic behaviour. Sears *et al.* (2000) found that Gambian children with a living maternal grandmother have better chances of survival than other children (Kurland & Gaulin 2005). Further, there exist no known methodological biases that would have caused the participants to report their altruistic tendencies, emotional closeness, empathic concern and contact frequency in ways that all correspond precisely with our *a priori* theoretical predictions.

In conclusion, our results support the hypothesis that humans have evolved psychological adaptations regulating discriminative altruism towards cousins that are sensitive to varying numbers of paternity uncertainty links, which characterize the distinct cousin categories. The current research is important because it shows that the laterality bias resulting from paternity uncertainty exists not only in investment in kin of the next generations, as others have demonstrated, but also in kin altruism towards the same generation, which this study is the first to demonstrate. The current study reveals an important theoretically predicted design feature of cousin relationships, and consequently contributes to a growing body of literature of kinship adaptations.

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APPENDIX A. THE MODEL OF COUSIN ALTRUISM

We explore how a focal individual's altruistic effort towards each category of cousins is related to the varied levels of paternity in the parental generation, based on Houston's (1995) framework of optimal paternal effort. Let x be the level of effort a focal individual invests in an altruistic act towards a certain recipient (who is the actor's cousin). We assume that $0 \leq x \leq 1$. We denote $F(x)$ as the recipient's reproductive success due to the altruistic act and $G(x)$ as the reproductive success of the actor from investing into cousins other than the recipient or not investing at all. Clearly, $F(x)$ will be an increasing function of x and $G(x)$ will be a decreasing function of x. The focal actor's inclusive fitness W by investing into a certain putative cousin can be written as follows:

$$W(x) = \frac{\rho}{8}F(x) + G(x), \tag{A 1}$$

where the recipient's fitness change is weighted by the genetic relatedness between the cousins, 1/8, and ρ is the probability that the recipient is the actor's genetically related cousin. Note that, if the focal actor were to have only one category of cousins, $G(x)$ could be written as $\rho G_0(x)$. In that case, it is clear that the optimal effort x^* into a putative cousin does not depend on ρ. Since it is impossible that our ancestors have had only one category of cousins throughout the evolutionary history, we can safely disregard this possibility.

A necessary condition for the optimal effort x^* is found by differentiating equation (A 1) with respect to x,

$$\frac{\rho}{8}F'(x^*) + G'(x^*) = 0, \tag{A 2}$$

where prime denotes differentiation with respect to x. The following second-order condition should also be satisfied in order for $W(x)$ to have a maximum at x^*,

$$\frac{\rho}{8}F''(x^*) + G''(x^*) < 0. \tag{A 3}$$

Differentiating implicitly equation (A 2) with respect to ρ, we can figure out how x^* changes with ρ,

$$\frac{dx^*}{d\rho} = -\frac{F'(x^*)}{\rho F''(x^*) + 8G''(x^*)}. \tag{A 4}$$

Reflecting equation (A 3), it is obvious that the optimal effort x^* is positively related to ρ, the probability that one's putative cousin is indeed one's genetically related cousin. Denoting P as the population-average within-pair paternity, we see that ρs for MoSis children, MoBro children, FaSis children and FaBro children are $1 : P : P : P^2$, respectively (figure 1). Since reduced ρ results in reduced optimal effort x^* into altruism towards cousins, the optimal efforts x^* towards distinct cousin categories are $x^*_{\text{MoSis}} > x^*_{\text{MoBro}} = x^*_{\text{FaSis}} > x^*_{\text{FaBro}}$.

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