Evolutionary Psychology

www.epjournal.net – 2009. 7(1): 118-132

Original Article

Biologically Costly Altruism Depends on Emotional Closeness Among Step but not Half or Full Siblings

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Abstract: We studied altruistic behaviors of varying biological cost (high, medium, and low) among siblings of varying genetic relatedness (full, half, and step). In agreement with inclusive fitness theory, the relative importance of either reliable (such as co-residence) or heuristic (such as emotional closeness) kinship cues depended crucially on the costs of help. When help did not endanger the altruist's life, thus making reciprocation possible, emotional closeness was the strongest predictor of altruism; perceived physical and psychological similarity to the sibling amplified altruistic behavior via their association with emotional closeness. When help endangered the altruist's life, thus making reciprocation unlikely, the strongest predictor of altruism was the ancestrally valid kinship cue of co-residence duration. Emotional closeness predicted costly altruism only for step siblings; its effects were non-significant when siblings were genetically related. Our findings support the idea that emotional closeness promotes costly altruistic behavior by serving as a surrogate kinship cue when more reliable cues are missing.

Keywords: altruism, siblings, kin selection, perceived similarity, emotional closeness.

Introduction

The theory of inclusive fitness suggests that a gene causing its bearer to help close relatives will be positively selected, provided that the benefits conferred to these relatives (multiplied by the coefficient of relatedness, i.e., by the probability that they also carry that gene) outweigh the costs incurred by the bearer (Hamilton, 1964). Although more acts of everyday altruism are directed to friends than to relatives (e.g. Stewart-Williams, 2007), things go differently when the costs of altruism are higher. If help is biologically significant (for example, donating a kidney rather than simply giving someone a little spare change), people do indeed prefer to help relatives—not only more than nonrelatives (Burnstein, Crandall, and Kitayama, 1994; Sime, 1983), but also more than friends (Stewart-Williams, 2007). This suggests that, in agreement with the principle of inclusive fitness, the relationship between genetic relatedness and helping behavior depends crucially on the costs (and proportional benefits) of the altruistic act. The first purpose of the present study was to examine helping behaviors varying in cost (high, medium, and low) among siblings varying in genetic relatedness (full, half, and step).

Costs of Helping

We distinguished four types of help. High-cost help (*life-saving altruism*) covers extreme behaviors that can save the life of the recipient but also threaten the life of the donor: it includes acts of self-sacrifice, such as donating a kidney, and bravery in the face of danger, such as entering a burning building to perform a rescue. Medium-cost help (*extra-ordinary altruism*) include extreme behaviors that imply sacrifice on the part of the donor, but are not life threatening: for example, giving someone a large amount of money. Low-cost help (*unconditional everyday altruism*) concerns behaviors whose costs and effects on fitness are trivial, such as giving someone a small gift. Life-saving, extra-ordinary, and everyday altruistic behaviors all involve giving help unconditionally, that is, without the expectation of anything in return. The lowest-cost type of altruistic behavior (*conditional everyday altruism*) involves offering biologically inexpensive help with the explicit expectation of receiving help back at some point in the future.

Relatedness of Siblings

Hamilton's inclusive fitness rule implies that altruism toward full siblings, whose probability of sharing the "altruism gene" by common descent is 0.5, would have had a very good chance of evolving by kin selection; altruism toward half siblings, whose probability of sharing the "altruism gene" by common descent is 0.25, would have had a smaller chance; and altruism toward step siblings, whose probability of sharing the "altruism gene" by common descent is zero, would have had no realistic chance of evolving by kin selection (see also Park, 2007). There are good reasons to believe that, as in present-day tribal societies (Hill and Hurtado, 1996), it was common for ancestral women to have children by different men, as a result of either extramarital mating or serial marriages. Thus, distinguishing between siblings of different genetic relatedness may have been a recurrent selection pressure throughout human evolutionary history (Buss, 1999). Accordingly, a second purpose of our study was to examine how different types of altruism may be influenced by different types of kinship cues.

Because genetic relatedness cannot be detected directly, one's siblings can be identified only probabilistically, on the basis of indirect cues; two of them have been shown to be far more important than consciously held beliefs about genetic relatedness itself (Lieberman, Tooby, and Cosmides, 2007). The first is maternal perinatal association, whereby individuals label as "sibling" any infant that they have observed in stable association with their own mother. Although this is probably the single most informative cue, it can only be used by older siblings, because younger siblings were not alive at the time their older siblings were born and nursed. A second, more universal cue is the duration of co-residence during the period of parental investment. In the ancestral environment, this cue would have been a reliable predictor of genetic relatedness because, particularly among foragers, children maintain close association with their mothers, and hence with their siblings, during childhood.

However, neither cue could possibly allow discrimination between full siblings and maternal half siblings. A mechanism that might be able to assist is phenotype matching, the estimation of relatedness through the comparison of an individual's appearance to a kin template (e.g., Wells, 1987). Humans do seem to use phenotype matching as a cue of kinship, and there is evidence that information about the self supersedes information about close family members in the kin template (Bressan and Zucchi, 2009), which would indeed aid discrimination between siblings of different relatedness. Phenotype matching might be based on physical features, such as facial similarity; for example, people are more likely to trust, and cooperate with, pictured partners whose face has been subtly manipulated to resemble them (see DeBruine, Jones, Little, and Perrett, 2008, for a review). Phenotype matching might also be based on non-physical traits, such as shared attitudes. It has been shown that people are more willing to help a fictional individual described as attitudinally similar to themselves than one described as dissimilar; furthermore, attitudinally similar individuals are implicitly associated to words denoting kinship (Park and Shaller, 2005).

Because many physical and attitudinal traits are heritable, relatives do tend to be physically and attitudinally more similar than strangers. Hence, it makes sense that perceived physical and attitudinal (or, more generally, psychological) similarity can serve as a heuristic kinship cue. Usually, relatives live together; given that extended interaction tends to generate emotional closeness, relatives are more likely than strangers to feel emotionally close to one another, too. Therefore, emotional closeness might also serve as a heuristic kinship cue (Neyer and Lang, 2003). This is consistent with the finding that people's willingness to help kin is partly mediated by feelings of emotional closeness (Korchmaros and Kenny, 2001, 2006).

Interactions Between Costs of Helping and Relatedness of Siblings

All indirect relatedness cues are fallible, but some are more fallible than others. When phenotypic similarity and emotional closeness are missing, maternal perinatal association and co-residence remain reliable cues of siblinghood, but not the other way around. An individual who was nursed by my mother and has been raised with me is likely to be a sibling, even if we are dissimilar in many respects and do not feel emotionally close to one another. However, an individual who has no association with my mother and has never resided with me is unlikely to be a sibling, regardless of any warm feelings between us, and regardless of whether we share attitudes or eye colors. Based on inclusive fitness theory, then, we should expect that more reliable kinship cues (such as co-residence) influence fitness-relevant altruism more than less reliable ones (such as phenotypic similarity and emotional closeness).

A gene causing its bearer to help another person can prosper even if the two individuals are genetically unrelated, as long as the relationship between them is such that the costs to the donor are smaller than the benefits that can be expected to be received in the future (Trivers, 1971). Although altruistic behaviors that do not threaten the life of the donor (an altruistic act can be directly repayed only if the donor continues to live) should be primarily driven by the likelihood that help is reciprocated in the future, the issue of reciprocation is explicit only when help is conditional. When help is unconditional, the probability that it is later reciprocated must depend on contingent factors such as residential proximity and frequency of contact, and even more on emotional closeness and the ensuing trust (see Humphrey, 1997). When help is conditional, the expectation that it will be later returned is part of the deal, and for this reason it should be influenced by neither contingent factors nor emotional closeness.

Hypotheses

On the basis of the above theoretical grounds, we offer the following hypotheses.

Hypothesis 1. When the life of the donor is not at stake, emotional closeness should drive unconditional altruism but not conditional altruism.

Hypothesis 2. When the life of the donor is at stake, reliable kinship cues (such as co-residence) should supersede heuristic kinship cues (such as emotional closeness, phenotype similarity, and even consciously held beliefs in relatedness).

This yields two separate predictions. First, co-residence should have a significant effect on life-saving altruism: more specifically, half siblings who have been raised together should be as willing to risk their life for one another as full siblings are. Second, for siblings who have co-resided—whatever their actual genetic relatedness, or more precisely their belief about it—emotional closeness and phenotypic similarity should *not* have a significant effect on life-saving altruism.

Hypothesis 3. When the life of the donor is at stake, heuristic kinship cues should be relied upon only when reliable kinship cues are missing.

Hence, emotional closeness may influence the willingness to offer life-saving help among unrelated individuals (such as step siblings) but not among related ones (such as half and full siblings).

Materials and Methods

Participants

Participants were 170 undergraduates at a university in the Midwestern USA, who received extra credit for their participation. They were recruited by an announcement that specified that participants should have at least one full, half, or step sibling. Twin pairs were excluded. Thirty-seven (21%) of the participants were male and 133 (79%) were female. Their average age was 20.8 years, while their siblings' average age was 20.2 years.

Materials

We prepared a questionnaire that contained a number of demographic questions and four scales (one on physical similarity, three on altruism, and one on emotional closeness), to be completed with a sibling in mind. The demographic questions also allowed us to assess residential proximity between respondent and sibling (on a 6-point scale, from 1=same city, to 6=more than 1000 miles); frequency of contact, as a combined measure of how often the participant sees, calls, or receives calls from the sibling (all rated on 5-point scales, from 1=hardly at all, to 5=extremely much); and, for half and step siblings, total length of co-residence (in months).

The three altruism scales, presented in counterbalanced order, measured unconditional everyday help, conditional everyday help, and extreme help. The scale for measuring *unconditional everyday altruism* (Cronbach's α=0.79) was an adaptation of the Self-Report Altruism Scale (Rushton, Chrisjohn, and Fekken, 1981), that in its original form asks participants to determine their likelihood of performing certain behaviors for a variety of related and unrelated individuals. We modified the scale, which has been shown to correlate very little with measures of social desirability, so that each question concerned altruistic behavior toward a sibling. The seven items of the scale referred to everyday, biologically inexpensive altruistic behaviors (e.g., giving small amounts of money without expecting to get it back or buying a sibling gifts without concern for receiving gifts in return), whose frequency respondents were instructed to rate (from 1=never, to 5=very often). The scale for measuring *conditional everyday altruism* (α=0.60) included the same statements, but it was specified that the help was conditional rather than unconditional (for example, "*I have given money to my sibling, only when I expected to get it back*"); again, respondents were asked to rate the frequency (from 1=never, to 5=very often).

We measured extreme altruism with an adaptation of Cunningham's (1986) altruistic scenarios. The scenarios concern three different categories of extreme, biologically relevant altruism: self-sacrifice (such as donating a kidney), generosity (such as co-signing a loan for a large amount of money), and bravery in the face of danger (such as entering a burning building to perform a rescue). We used four scenarios (α=0.85) concerned with *life-saving help* at own peril (self-sacrifice and bravery in the face of danger) and four scenarios (α=0.79) concerned with *non-life-saving help* (generosity, mainly monetary); participants were asked to determine their likelihood of helping their sibling in each (from 1=not at all likely, to 5=extremely likely).

To estimate emotional closeness, we used 30 items from the warmth scale of the Adult Sibling Relationship Questionnaire (ASRQ; Stocker, Lanthier and Furman, 1997). This full scale assesses attitudinal similarity, intimacy, affection, admiration, emotional support, instrumental support, acceptance, and knowledge. A sample item would be, "How much do you think of this sibling as a good friend?" (from 1=hardly at all, to 5=extremely much). The *emotional closeness* score was the mean of the ratings given to the intimacy (α=0.94), affection (α=0.93), admiration (α=0.85), acceptance (α=0.87), and knowledge (α=0.91) subscales; each of these scales contained six items. The emotional support and instrumental support subscales were excluded because they partly overlapped with the altruism measures. The *psychological similarity* score (α=0.91) was the mean of the ratings given to the 4 items of the attitudinal similarity subscale, covering similarity in interests, personality, way of thinking, and lifestyles.

The *physical similarity* scale (α=0.90), based upon Cohen, Dibble, Grawe, and Pollin's (1973) scale to measure zygosity among twins, consisted of 12 Likert-style questions regarding a variety of physical traits (height, weight, body structure, and coloring, in addition to overall physical characteristics) in which participants were asked to rate how much they were similar to their sibling (from 1=hardly at all, to 5=extremely much).

Procedure

Participants were asked to complete the questionnaire with their sibling (or one of their siblings, if they had more than one) in mind. We made sure that participants singled out one specific sibling by asking them, when signing up for the study, to bring a photograph of this sibling to the testing site. One hundred and three (60.5%) participants completed the questionnaire according to their relationship with a full sibling, 40 (23.5%) with a half sibling, and 27 (15.9%) with a step sibling.

Results

Table 1 displays the means and standard errors for the most important variables, separately for each sibling type (full, half, and step).

Table 1. Means and standard errors (within brackets) for the main measures, for full (*N*=103), half (*N*=40), and step (*N*=27) siblings.

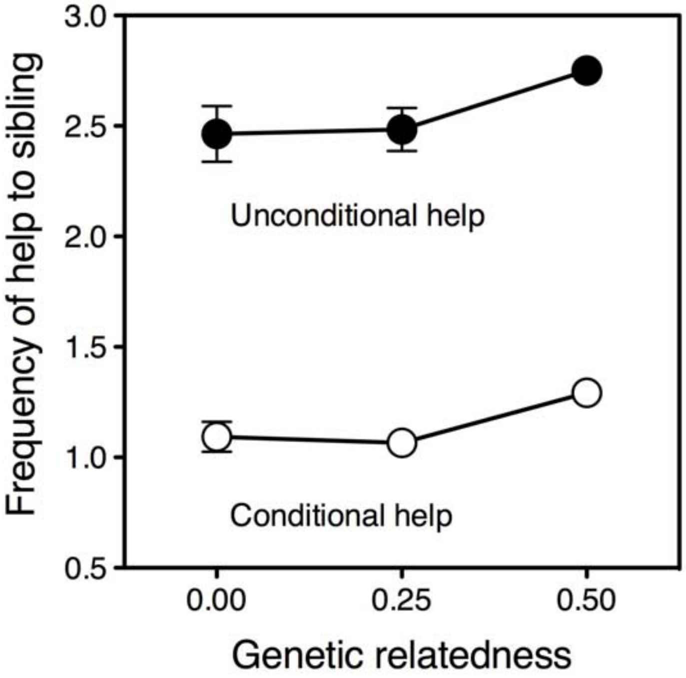
	Type of sibling		
Variable	Full	Half	Step
Contact frequency	2.83 (0.08)	2.31 (0.14)	1.89 (0.15)
Emotional closeness	3.80 (0.06)	3.36 (0.14)	2.85 (0.15)
Physical similarity	3.03 (0.09)	2.30 (0.13)	1.78 (0.09)
Psychological similarity	3.33 (0.09)	2.77 (0.18)	2.33 (0.19)
Extreme help (life-saving)	4.54 (0.07)	4.42 (0.14)	3.52 (0.21)
Extreme help (non-life-saving)	4.00 (0.09)	3.60 (0.18)	2.75 (0.18)
Everyday help (unconditional)	2.91 (0.07)	2.39 (0.13)	1.94 (0.15)
Everyday help (conditional)	1.27 (0.04)	1.08 (0.03)	1.14 (0.04)

Genetic Relatedness and Everyday Help

We performed a multivariate analysis of covariance (MANCOVA) using type of everyday help (conditional, unconditional) as the dependent variable and type of sibling (step, half, full) as the independent variable. As covariates, we entered emotional closeness (Korchmaros and Kenny, 2001) and other six factors known to influence sibling relationships (Neyer and Lang, 2003; White and Reidman, 1992): (a) gender, (b) sibling gender, (c) age, (d) sibling age, (e) residential proximity, and (f) frequency of contact. Covariance-adjusted means of frequency of everyday help given to sibling are shown in Figure 1.

Type of sibling (step, half, full) was significant as a main effect, $F(2, 157)=7.20$, $p=0.001$. Pairwise comparisons showed that half and step siblings differed from full siblings ($ps \leq 0.006$) but not from each other ($p=0.98$). Type of everyday help was also significant as a main effect, $F(1, 157)=4.32$, $p=0.039$; however, it interacted significantly with age, sibling age, frequency of contact, and emotional closeness (all $Fs(1, 157) \geq 6.86$, $ps \leq 0.01$). To investigate the nature of these interactions, we ran two separate analyses of covariance (ANCOVAs) on the two types of help. The frequency of unconditional everyday help was influenced by age of participant, $F(1, 158)=7.11$, $p=0.008$, with older participant helping their siblings more than younger participants; age of sibling, $F(1, 158)=6.02$, $p=0.015$, with younger siblings being helped more than older ones; contact frequency, $F(1, 158)=9.18$, $p=0.003$, with more help given to siblings that participants see or call more often; and especially emotional closeness, $F(1, 158)=26.27$, $p<0.0001$, with more help given to siblings towards whom participants have warmer feelings. The frequency of conditional everyday help was influenced by none of the above factors (all *p*s≥0.23).

Figure 1. Covariance-adjusted mean frequency of conditional and unconditional everyday help given to sibling (on a 1-to-5 scale), as a function of the sibling's genetic relatedness coefficient. Error bars indicate standard errors.



For each sibling type, we examined the relative impact on unconditional everyday altruism of our covariates (emotional closeness, gender, sibling gender, age, sibling age, residential proximity, and frequency of contact) by entering them into stepwise multiple regressions, as independent variables. For half and step siblings, to these variables we added length of co-residence (i.e., number of months spent in the same household).

Among full siblings, residential proximity (siblings living nearby were more likely to be helped) and frequency of contact (siblings seen or called more often were more likely to be helped) were significant predictors of everyday altruism, but added little to the effect of emotional closeness, that alone explained 34% of the variance (multiple regression, overall r^2=0.44, *F*(3, 98)=25.33, *p*<0.0001; effect of emotional closeness: *ß*=0.42, *t*=4.47, *p*<0.0001; effect of residential proximity: *ß*=0.22, *t*=2.74, *p*=0.007; effect of contact frequency: *ß*=0.22, *t*=2.22, *p*=0.029).

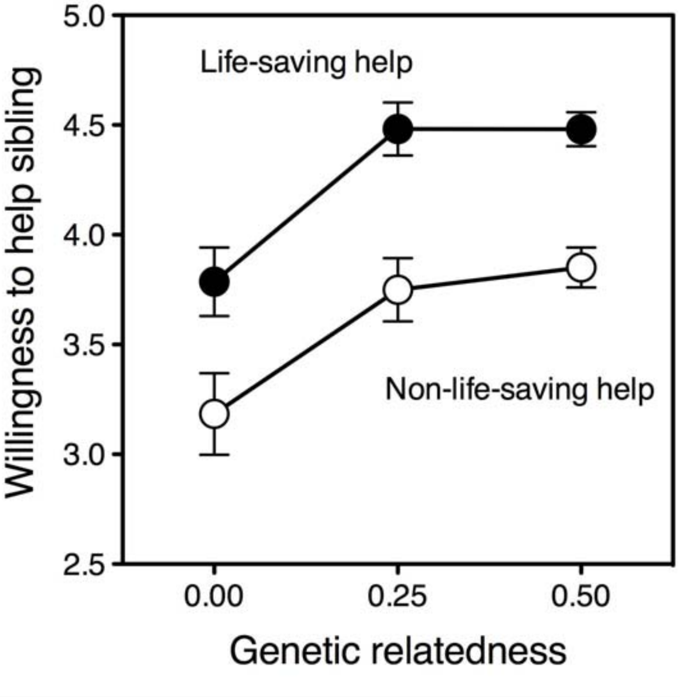
Among half siblings, residential proximity (siblings living farther away were more likely to be helped) was a significant predictor of everyday altruism, but added little to the effect of emotional closeness, that alone explained 35% of the variance (multiple regression, overall r^2=0.48, *F*(2, 36)=16.43, *p*<0.0001; effect of emotional closeness: *ß*=0.68, *t*=5.49, *p*<0.0001; effect of residential proximity: *ß*= -0.37, *t*= -2.99, *p*=0.005).

Among step siblings, co-residence (siblings who had cohabited longer with the participant were more likely to be helped) was a significant predictor of everyday altruism, but added little to the effect of emotional closeness, that alone explained 34% of the variance (multiple regression, overall r^2=0.45, $F(2, 23)$=9.44, p=0.001; effect of emotional closeness: β=0.49, t=3.03, p=0.006; effect of co-residence: β=0.35, t=2.15, p=0.042). The significant effect of co-residence was entirely driven by (the only) two participants who had cohabited with their step siblings all their life: a woman of 20, with had co-resided for 20 years with her 23-year-old step sister, and a woman of 19, who had co-resided for 18 years with her 18-year-old step brother. If these two participants were excluded from the analysis, emotional closeness was the only significant predictor, and this single-factor model explained 35% of the variance (effect of emotional closeness: β=0.59, t=3.45, p=0.002).

Genetic Relatedness and Extreme Help

We performed a multivariate analysis of covariance (MANCOVA) using type of extreme help (life-saving, non-life-saving) as the dependent variable, and type of sibling (step, half, full) as the independent variable. As before, we entered as covariates emotional closeness, gender, sibling gender, age, sibling age, residential proximity, and frequency of contact. Covariance-adjusted means of likelihood to give extreme help to sibling are shown in Figure 2.

Figure 2. Covariance-adjusted mean likelihood to give life-saving and non-life-saving (mainly monetary) extreme help to sibling, on a 1-to-5 scale, as a function of the sibling's genetic relatedness coefficient. Error bars indicate standard errors.



Type of sibling (step, half, full) was significant as a main effect, $F(2, 158)$=8.80, p<0.0001. Pairwise comparisons showed that full and half siblings differed from step siblings (ps≤.001) but not from each other (p=0.71).

Type of extreme help was significant both as a main effect, $F(1, 158)$=12.93, p<0.0001, and in interaction with emotional closeness $F(1, 158)$=7.40, p=0.007. Separate

ANCOVAs showed that this interaction was due to the fact that the effect of emotional closeness was significant in non-life-saving contexts (i.e., extra-ordinary generosity: $F(1, 158)=10.45$, $p=0.001$), and nonsignificant in life-saving help contexts (i.e., saving the sibling at own peril: $F<1$, $p=0.55$).

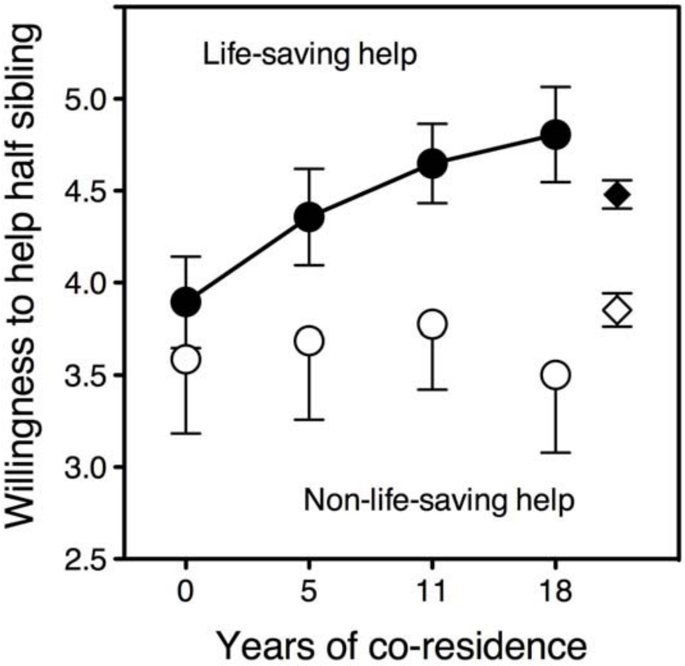
For each sibling type, we examined the relative impact on life-saving altruism of our covariates (emotional closeness, gender, sibling gender, age, sibling age, residential proximity, and frequency of contact) by entering them into stepwise multiple regressions, as independent variables. For half and step siblings, to these variables we added length of co-residence (i.e., number of months spent in the same household).

Among full siblings, frequency of contact (siblings seen or called more often were more likely to be helped) and sibling age (younger siblings were more likely to be helped) were the only variables that significantly predicted life-saving altruism, although the regression model explained only 13% of the variance (multiple regression, overall $r^2=0.13$, $F(2, 99)=7.63$, $p=0.001$; effect of contact frequency: $\beta=0.26$, $t=2.79$, $p=0.006$; effect of sibling age: $\beta= -0.24$, $t= -2.56$, $p=0.012$).

Among half siblings, exactly the same variables (frequency of contact and sibling age) were significant, but they were trumped by co-residence duration, that was the most important predictor. The regression model explained 37% of the variance (multiple regression, overall $r^2=0.37$, $F(3, 35)=6.72$, $p=0.001$; effect of co-residence: $\beta=0.44$, $t=3.14$, $p=0.003$; effect of sibling age: $\beta= -0.39$, $t= -2.80$, $p=0.008$; effect of contact frequency: $\beta=0.30$, $t=2.22$, $p=0.033$).

To analyze the role of co-residence in more detail, we used co-residence duration as a between-subjects factor in an ANCOVA, dividing our participants into four equal groups (see Figure 3) according to number of months of co-residence (data from one participant were excluded because co-residence information was missing). The four groups included participants who had lived together: zero months, i.e., never (25th percentile and lower, 10 participants); 1-108 months, i.e., on average 5 years (from the 25th to the 50th percentile, 10 participants); 109-168 months, i.e., on average 11 years (from the 50th to the 75th percentile, 10 participants); and 168-252 months, i.e., on average 18 years (higher than the 75th percentile, 9 participants). Pairwise comparisons showed that participants who had spent 109 months (9 years) or longer in the same household as their half siblings were significantly more likely to help them in a life-saving context than participants who had never lived with them (ps≤0.039).

Figure 3. Covariance-adjusted mean willingness to give life-saving and non-life-saving (mainly monetary) extreme help to half sibling, on a 1-to-5 scale, as a function of mean length of time spent in the same household. Error bars indicate standard errors; in the lower data set, top halves of error bars are not shown to avoid crowding. Corresponding means for full siblings are shown on the right (diamond symbols).



Emotional closeness was not a significant predictor for either full siblings (β= -0.07, $|t|<1$) or half siblings (β=0.05, $|t|<1$). On the contrary, emotional closeness was the *only* significant predictor for step siblings, and this single-factor model explained 23% of the variance (effect of emotional closeness: β=0.48, t=2.64, p=0.014).

Perceived Physical and Psychological Similarity

Perceived physical and psychological similarity correlated positively with genetic relatedness, even when controlling for absolute age difference (both rs≥.34, p<.0001).

Perceived physical similarity was positively associated with emotional closeness (r=0.31, p<0.0001, n=162, controlling for relatedness). The more similar a sibling's smile, nose, lips, cheekbones (all rs>0.21, ps<0.006, controlling for relatedness), and to a lesser extent height and body structure were judged to be, the warmer the feelings toward that sibling. The only feature that did not correlate significantly with emotional closeness was similarity in eye color. However, the relationship between perceived physical similarity and emotional closeness was mediated by perceived *psychological* similarity, as shown by the fact that their correlation (r=0.31) became nonsignificant (r=0.02) when psychological similarity was statistically removed.

We repeated all our analyses with perceived physical and psychological similarity to the sibling included as either covariates (ANCOVAs) or independent variables (regressions). This inclusion did not affect any of the results. In fact, perceived physical and psychological similarity correlated positively and significantly with all three types of unconditional altruism (all rs>0.22, ps<0.005), but correlations became nonsignificant when emotional closeness was controlled for (all rs<0.12, ps≥0.12).

Interestingly, whereas the effects of psychological similarity on *everyday* unconditional altruism were essentially the same in all sibling groups (correlations ranged from .41 to .54, all ps<.004), its impact on *extreme* altruism increased steadily with increasing genetic distance between the siblings (the correlation raised from r=0.09, p=0.35, for full siblings, to r=0.23, p=0.16, for half siblings, peaking at r=0.49, p<0.01, for step siblings; the first and third correlations are significantly different, Z test, p=0.05). In other words, psychological similarity had a significant effect on biologically relevant, extreme altruism (via emotional closeness) only when donor and recipient were *not* genetically related.

Discussion

Biologically Inexpensive Altruism Depends on Emotional Closeness, Whether or not Kinship Cues Are Present

We found more conditional altruism among full than among half or step siblings. Unexpectedly high levels of reciprocity among relatives (siblings and cousins) have been reported by Stewart-Williams (2007) in terms of significant correlations between help given and help received. He suggested that unreciprocated kin altruism might be most common when there is an asymmetry in the neediness and/or reproductive value of the parties involved, such as in the parent-offspring relationship. Siblings have usually similar ages and therefore similar needs and reproductive values; under these circumstances, reciprocal altruism may make more sense than unreciprocated altruism. However, our finding that conditional altruism is more frequent among full than among half and step siblings (when the age of both parties is partialled out, together with gender, emotional closeness, residential proximity, and contact frequency) cannot be explained in this way. Also, among full siblings we found not only more conditional altruism, but also more *un*conditional altruism. The latter result is consistent with the finding that levels of social investment, in terms of concern given and received, are higher for full than for half siblings (Pollet, 2007).

Although conditional everyday help is offered with the *explicit* expectation of receiving help back at a later time, unconditional everyday help may be offered with the implicit, and not necessarily conscious, expectation that help will be returned if and when the need arises. The chances that the altruist gets a future return of benefits depends, of course, on whether the person who has been helped remains close, so as to be able to reciprocate at the right moment (Humphrey, 1997). Thus, a possible explanation of our finding is that full siblings are more likely to maintain close contact than less related siblings (Pollet and Nettle, 2009). Close contact is bound to increase both the implicit and the explicit confidence that help can be later reciprocated, hence the inclination to help both unconditionally *and* conditionally. Consistent with hypothesis 1, we found that emotional closeness influenced unconditional, but not conditional, altruism. This result supports the idea that emotional closeness increases the probability that unconditional help will be reciprocated.

Biologically Costly Altruism Does Not Depend on Emotional Closeness When Kinship Cues Are Present

We found that, in life-or-death contexts, full siblings and half siblings with whom participants had cohabited (the longer, the better) were helped most willingly; half siblings with whom participants had never cohabited and step siblings were helped least willingly. These preferences were independent of the degree of emotional closeness between siblings.

We did not collect information about whether half siblings were maternal or paternal, and this is a limitation of our study. However, this factor is inevitably conflated with co-residence (e.g. Pollet, 2007), because children tend to remain with their mothers when their parents separate. This problem persists even when co-residence is apparently controlled for, as shown by the finding that, in a polygamous community, children displayed higher practical and emotional solidarity toward full siblings than toward paternal half siblings. Even though all siblings were raised in close proximity, mothers could not help fostering a "uterine" family within the big family (Jankowiak and Diderich, 2000).

Burnstein et al. (1994) reported that, in life-or-death scenarios, people chose to aid closer kin over more distant kin. Participants ranked the members of a hypothetical triad of target individuals varying in degree of relatedness to themselves; the difference in willingness to help 50%- and 25%-related kin was statistically significant. Our findings complement Burnstein et al.'s by suggesting that there is more to siblinghood than the proportion of shared genes. When the recipients and their relatedness to the respondent are imaginary ("your brother's 3-day-old son", "your 18-year-old female cousin"), as in Burnstein et al.'s study, hypothetical altruism was completely determined by belief in relatedness. When the recipients are real siblings, however, belief in relatedness is supplanted by an ancestrally valid kinship cue: co-residence. Our findings are in accord with the hypothesis that, unconsciously, humans use co-residence as a cue to estimate genetic relatedness—regardless of their consciously held beliefs about the latter (Lieberman et al., 2007). Consistent with hypothesis 2, the length of co-residence with a half sibling significantly increased the probability of acting altruistically towards him or her at high personal cost, *independently* of any increased emotional closeness that co-residence brought about.

Biologically Costly Altruism Depends on Emotional Closeness When Kinship Cues Are Missing

We found that perceived physical and psychological similarity correlated strongly and positively with genetic relatedness. This might seem unsurprising, but in apparent contradiction, Kruger (2003) reported that genetic relatedness was *negatively* related to a measure of psychological similarity such as "oneness." However, in that study siblings were contrasted with friends. Friendships are largely formed on the basis of perceived similarity (see also Rushton, 1989). Our data show that, other things being equal, increased genetic distance involves decreasing feelings of similarity.

Perceived physical similarity was positively associated with altruism. The importance of physical similarity, especially in facial features, complements the evidence that a father's perception of the degree of physical resemblance with his child is positively associated with the quality of their relationship (Apicella and Marlowe, 2004; Burch and

Gallup, 2000), and that success in adoptions correlates with the similarity in mannerisms and temperament between child and foster parents, as estimated by the parents (Jaffee and Fanshel, 1970). However, the impact of physical similarity on altruism was not direct (as one would expect if physical similarity were used as a conscious or unconscious cue to genetic relatedness), but indirect, via psychological similarity. A correlation between perceived physical similarity and feelings of "social closeness" has been reported on reunited (both identical and fraternal) twin pairs (Segal, 2003). The connection between perceived physical similarity and psychological similarity is also reminiscent of the finding that strangers with self-resembling faces look especially trustworthy (DeBruine, 2002). Physical similarity might hence encourage feelings of psychological similarity.

The impact of psychological similarity on extreme altruism was large and significant in step siblings, much smaller in half siblings, and virtually zero in full siblings. This suggests that whereas genetic relatedness promotes altruistic behavior largely independently of psychological similarity, psychological similarity may serve, between unrelated individuals, as a replacement for genetic relatedness itself. This idea is consistent with the finding that people implicitly associate fictional individuals described as attitudinally similar to themselves with kinship concepts, such as brother or family (Park and Shaller, 2005). There is evidence that even superficial resemblances, such as a shared name or surname, can increase altruism towards strangers (Oates and Wilson, 2002). Our data suggest that they might do so by creating a feeling of emotional closeness; in our study, the effects of similarity on altruism essentially vanished when emotional closeness was taken out of the equation.

Consistent with hypothesis 3, we found that a heuristic kinship cue such as emotional closeness influenced the willingness to offer biologically costly help among unrelated individuals (such as step siblings) but not among related ones (such as half and full siblings). In other words, cues that are only loosely associated with genetic relatedness become effective only when reliable kinship cues are missing.

Conclusions

We have shown that altruism among siblings is influenced by both genetic relatedness and emotional closeness. The relative importance of these two components depends on the context in ways that are consistent with the principle of inclusive fitness. In situations involving self-sacrifice, altruism is largely independent of feelings of emotionally closeness if donor and recipient are likely to be genetically related (i.e., have been raised together), but depends crucially on such feelings if donor and recipient are unlikely to be related (i.e., have never cohabited). Blood is indeed thicker than water when chances are that it would be shed; but emotional closeness can take the place of missing genetic ties among unrelated individuals. And when life and death are not directly at stake, unconditional altruism is driven by the emotional closeness that relatedness tends to entail, rather than by relatedness itself.

Acknowledgements: Part of this research was submitted as a Master's thesis by Mary Beth Cavalieri to the Department of Psychology at Central Michigan University, Mt. Pleasant, MI. Portions of this paper were originally presented in 2003 at the meetings of the Human Behavior and Evolution Society and of the American Association for the Advancement of Science.

Received 08 October 2008; Revision submitted 10 March 2009; Accepted 11 March 2009

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