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Original Article

Hamilton's rule predicts anticipated social support in humans

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Hamilton's rule predicts that individuals should be more likely to altruistically help closer kin and this theory is well supported from zoological studies of nonhumans. In contrast, there is a paucity of relevant human data. This is largely due to the difficulties of either experimentally testing relatives or of collecting data on genuinely costly cooperation. We test Hamilton's rule in humans by seeing if the availability of help in times of crises is predicted by the degree of genetic relatedness. In social network research, the pool of people that one can go to for support during times of crisis is termed the support network. By definition, the members of a support network provide various benefits in times of need, and larger support networks have been shown to be important for general health. As this level of support bears costs for the providers and has clear benefits for the receivers, it therefore allows us to test Hamilton's rule. We use an Internet sample to analyze the composition of 540 people's support networks. We had people rank their support network members in order of who would be most likely to help and found that relatives were more likely to be ranked in primary positions and that the degree of relatedness correlated with rank.

Key words: **altruism, cooperation, kin selection, kinship, reciprocity, social networks.**

INTRODUCTION

Hamilton's rule predicts that individuals should be more likely to altruistically help closer kin and likewise, be more likely to receive help from closer kin (Hamilton 1964). In this context, human cooperation is often considered puzzling as human social networks comprise many interactions between relatives and nonrelatives, with kinship terms often plastic and extended to include nonrelatives (Fox 1967; Carsten 2000; Franklin and McKinnon 2001). Furthermore, many frequent acts of human cooperation and generosity occur between nonrelatives, such as food-sharing (Gurven 2004) or resource sharing, especially in laboratory experiments (Fehr and Fischbacher 2003). Therefore, it is sometimes argued that human altruism cannot be explained by Hamilton's rule, because it does not capture the important features of human sociality (Fehr and Fischbacher 2003; Gintis 2003; Gintis et al. 2003; Henrich et al. 2005; Bowles 2006; Wilson and Wilson 2007; Gintis et al. 2008; Nowak et al. 2010).

Hamilton's rule is well supported from zoological studies (Cornwallis et al. 2009, 2010, but see Nowak et al. 2010; Abbot et al. 2011), but there is a relative paucity of human data on the importance of Hamilton's rule (Madsen et al. 2007; Rushton 2009). Part of the difficulty in testing Hamilton's rule in humans is in gathering experimental data on human cooperation that is genuinely costly and that has fitness consequences for both actors and recipients. Ethical considerations prevent causing harm or distress and thus prevent creating a need for urgent support, and practical limitations make experiments on relatives more difficult to arrange. Therefore, human cooperation is typically studied using economic incentives among strangers facing moral dilemmas (Fehr and Fischbacher 2003). While the results of such studies showing cooperation among strangers are of interest, these studies provide limited scope for explaining the evolution of human altruism. This is because such experiments often entail trivial costs and do not test behavior between relatives. They therefore cannot test the relative importance of relatedness, and thus rather than providing an empirical refutation of Hamilton's rule (Fehr and Fischbacher 2003), they are merely unable to test it (West et al. 2011).

Perhaps the above mentioned difficulties, of creating a need for help, or recruiting relatives for studies, explain why much focus has been on cooperation within human friendships (Fiske 1991, 1992; Ackerman et al. 2007) or cooperation between strangers in the laboratory (Fehr and Fischbacher 2003). Therefore, the first study to directly test Hamilton's rule experimentally in humans was not until 2007 (Madsen et al. 2007) whose study

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allowed participants to endure painful exercise as a way of benefitting others. The benefits went to known individuals ranging in relatedness to the actor, in contrast to the typical experimental situation whereby benefits go to anonymous strangers (Fehr and Fischbacher 2003). Their results showed that individuals tended to endure more costs, in an experimental setting, when the benefits went to closer relatives, including themselves. However, the costs and benefits of the Madsen et al. (2007) study were neither large nor examples of naturally occurring behavior, and thus it could be argued that they are as artificially trivial as laboratory studies on social dilemmas.

Another method to investigate human cooperation is to observe social behaviors using naturalistic experiments in "the field" (Nettle et al. 2013) or with anthropological records of nonexperimental behavior (Essock-Vitale and Mcguire 1980). Such studies of human behavioral ecology have found mixed results for the role of relatedness and reciprocity (Gurven 2004; Allen-Arave et al. 2008). However, while such studies tend to have greater external validity than experimental studies, it remains that data relating to very costly acts of cooperation, or cooperation that provides a large benefit, can be hard to collect and test. An alternative to the experimental or behavioral ecology approaches is to study human sociality and cooperation with social network analysis (Hoyt and Babchuk 1983; Höllinger and Haller 1990; Wellman and Wortley 1990; Pollet et al. 2013), which measures the strength of ties and the frequency of interactions between individuals (Milardo 1992; Neyer and Lang 2003; Harrison et al. 2011) or households (Nolin 2010).

In social network research, the pool of people that one can go to for support during times of crisis is termed the Support Network (Cohen and Wills 1985). By definition, the members of one's support network provide "psychological and material assistance." Examples include but are not limited to; providing advice; helping to move house; lending money and food (Hadley et al. 2007); or looking after children and helping the infirm (reviewed in Cohen and Wills 1985). Such helping behaviors appear to have clear benefits for the receivers, such as immunity from food shortages, improved physical/mental health, and perhaps even decreased mortality (Umberson et al. 1996; Uchino et al. 2001, 2004; Cohen 2004; Dickens et al. 2004; Hadley et al. 2007; Holt-Lunstad et al. 2010). In contrast, such support is arguably costly for the providers (e.g., providing money or giving up time to provide help) and therefore can be used as a proxy measure for altruistic behavior in the Hamiltonian sense (Hamilton 1964).

We use an Internet sample to analyze the composition of 540 people's support networks. Importantly, we had people rank the members of their support network in order of who they would be most likely to seek help from first. We use this rank-ordered list as a proxy for the likelihood of help being provided if required and we test if this likelihood correlates with the degree of relatedness between the focal participant (Ego) and their network member (Alter).

To facilitate the synthesis of ultimate and proximate explanations for human behavior (Scott-Phillips et al. 2011; Nettle et al. 2013), we also test if people are emotionally closer to genetically closer relatives and if emotional closeness predicts the perceived likelihood of receiving help. This is because emotional closeness has been shown to psychologically drive helping behaviors and to affect the statistical association between relatedness and the willingness to help (Korchmaros and Kenny 2001, 2006).

METHODS

We follow standard practice in network analysis in referring to the focal "owner" of a network as Ego, and the individual members of their network as Alters (Hanneman and Riddle 2005).

Participants

We primarily recruited participants by using two website depositories (http://psych.hanover.edu/research/exponnet.html and http://www.socialpsychology.org/expts.htm). In total, there were 900 respondents that started the anonymous questionnaire and 540 individuals (428 female, 112 male) aged 18–69 years (mean age 27.7 ± 9.9 SD years) completed it. Of these, 427 were tertiary-educated, and 363 were in a romantic relationship. Participants were not rewarded for taking part (though they may have received course credits).

Our questionnaire solicited brief personal details (e.g., age, gender, and number of siblings), and then asked them to list all the people that they felt they could approach for help in times of "*severe emotional or financial crisis*" (following the method used by (Dunbar and Spoors 1995). Participants were asked to rank these individuals in terms of whom they would be most likely to approach (rank 1 highest). We took care to avoid biasing subjects toward any specific number of Alters, allowing them to specify however many they felt were important to them up to a maximum of 15 Alters. Obviously this questionnaire structure may have biased our participants' responses (Vehovar et al. 2008) but our 15 boxes was well beyond the expected mean number of five (Milardo 1992) and included the full range recorded by (Roberts et al. 2008) of 0 to 14 Alters.

Copy of the question we supplied to our respondents,

> Imagine you are suffering a very severe emotional or financial crisis.
>
> Please think of ALL the people you would be prepared to seek support or help from in such a crisis, and list their details below. Please rank them in order. Put the person you would be most likely to seek support or help from first, at the top. There are 15 rows but you should ignore this number and just answer the question as honestly as possible.

Respondents specified how emotionally close they felt toward each Alter, on a scale from 0 (no emotional closeness) to 10. They also specified if and how each Alter was related to them, and these relationships then were translated into standard estimated coefficients of genetic relatedness: r = 0.5 for parents, full siblings and offspring; r = 0.25 for grandparents, grandchildren, aunts/uncles, nieces/nephews and half-siblings; r = 0.125 for first cousins, great-grandparents, great aunts/uncles.

We recorded 7 demographic variables that we solicited at the start of the questionnaire as control covariates considered likely to affect the maximum number of relatives possible in a respondent's support network. We also controlled for relationship status as we expected that many people would turn to their romantic partner first in a crisis. The variables contained 3 continuous variables; age (which we standardized); number of offspring; number of siblings (including half-siblings but not step-siblings); and 5 categorical variables; gender (female/male); in romantic relationship (yes/no); father alive (yes/no); mother alive (yes/no) (see Table 1 for descriptive statistics of our sample). Unfortunately, we neglected to record the nationality of our respondents.

Table 1
Descriptive statistics of sample (*N* = 540)

	No/male	Yes/female
Categorical variables		
Gender	112	428
In relationship	177	363
Mum alive	47	493
Dad alive	105	435
Have offspring	367	173
In education	113	427
	Mean	SD
Continuous variables		
Age	27.73	9.867
Number of genetic siblings	2.64	2.18
Number of offspring	0.65	1.195

Statistical analyses

Measuring the role of relatedness within support networks: There are problems with using relatedness as a response variable as it could be argued to be a proportional response but the denominator is undefined. Therefore, we first tested if the mean level of relatedness correlated with rank by performing a weighted regression (sample means for each ranking position weighted by sample size). The weighting was necessary because the number of samples varied with rank (every Ego had an Alter at rank 1 by definition, but only a few listed 15 Alters). We also ran a mixed effects model to control for pseudo-replication emanating from the multiple alters of each ego (Hurlbert 1984), with relatedness treated as a proportional response (bounded between 0 and 0.5 in 4 units of 0.125), respectively. Of the fixed effects, we standardized Age by mean centering and dividing by the standard deviation. The random effects were random intercepts for each subject and random slopes for the rank variable, and the covariances of these random effects were unstructured where possible, to allow the intercept and slope to covary as expected with a bounded response variable. However, if model convergence was not achieved we simplified the random effects until convergence was reached. We report all the random effects in Tables 2–4.

Likewise we modeled the proportion of respondents that chose a particular type of Alter (e.g., related vs. unrelated) to "slot" into a particular rank. This way, we could test for significant trends across rank against the null model that a particular type of Alter was just as likely to be placed in any particular rank. We also tested if emotional closeness correlated with rank by modeling the degree of emotional closeness reported by Egos toward their Alters as a proportional response bounded between 0 (no closeness) and 10. Degrees of freedom were always approximated with the Satterthwaite method and because our models may be over-dispersed, we tested for the significance of fixed effects within models with robust estimations of covariances. However, we conducted our primary tests of interest by comparing different models with or without our variable of interest (rank in the support network) with likelihood ration tests (LRT). All analyses were conducted in IBM SPSS version 21.

For our figures, we use confidence intervals which are bootstrapped (1000 times), using sampling with replacement and bias correction with acceleration (BCa) for all Alters occupying the corresponding rank position, not controlling for Ego identity. The confidence intervals increase with rank because the sample size decreases.

Table 2
Generalized linear mixed effects models of the emotional closeness between an Ego and their Alters

Term	Model 1	Model 2
Intercept	1.208 (0.0128)***	1.332 (0.128)***
Gender (female)	0.216 (0.096)*	0.206 (0.093)*
Age (standardized)	−0.071 (0.050)	−0.079 (0.049)
Mum alive (no)	0.345 (0.130)**	0.370 (0.128)**
Dad alive (no)	−0.084 (0087)	−0.082 (0.084)
Number of genetic siblings	−0.004 (0.016)	−0.001 (0.016)
Offspring-binary (no)	−0.079 (0.093)	−0.095 (0.092)
In relationship (no)	−0.180 (0.066)**	−0.187 (0.064)**
Rank		−0.143 (0.011)***
Random effect covariances		
Subject intercept	0.048 (0.005)***	3.578 (0.318)***
Information criterion		
−2 log pseudo-likelihood	6823.069	6727.915
Akaike corrected	6825.071	6729.917
Bayesian	6831.017	6735.862
Likelihood ratio test (df)	n/a	95.154 (1)***
Number of observations (subjects)	2836 (540)	2836 (540)

Degrees of freedom calculated with Satterthwaite approximation option.
Tests of fixed effects use robust covariances.
Likelihood ratio test compares the change in −2 log pseudo-likelihood between nested models.
Emotional closeness modelled as a binomial-probit variable ranging from 0 to 10.
$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

RESULTS

General composition of support networks

Mean support network size was 5.25 ± 3.2 SD, the median was 4 and the mode was 3 (range 1–15) (Figure 1). Twenty-one respondents (4%) listed the maximum number of Alters possible (15), and 53 respondents (10%) listed no relatives within their support network. Of the 2836 Alters listed by the 540 respondents, 1435 (51%) were related to the respondent, and their mean relatedness coefficient was r = 0.422 (r = 0.225 overall), indicating that most such individuals were within the first degree of relatedness (r = 0.5). Parents comprised 30% of the Alters, and 70% of all alive parents were listed by egos in their support network (646 from a maximum 928 reported to still be alive). Although 49% of Alters were not related to Egos, this includes the 14% (398) of Alters who were either romantic partners (284), the family of such partners (65), or ex-partners (49). Overall, 21% (580) of the Alters co-habited with the ego, and 49% (1393) of the Alters lived in the same town/city as the ego.

The role of relatedness within support networks

Overall, Egos reported being emotionally closer to higher ranked Alters (LRT of GLMM: Xsq(1) = 95.154, P < 0.001, Table 2, Figure 2) and in support of Hamilton's rule, average relatedness decreased from rank 1 to 15 (weighted regression of rank means for relatedness: $F_{1,14} = 43.25$, $P < 0.001$, $R^2_{adj} = 0.75$; LRT of GLMM: Xsq(1) = 50.386, P < 0.001, Table 3, Figure 3a), although this could in part be explained by Egos simply placing relatives in general in the higher rankings, with no regard to their degree of relatedness (Figure 3b). However, if we restrict the analysis to related Alters only, the negative correlation between rank and relatedness is even clearer (weighted regression of rank means on related Alters only: $F_{1,14} = 267.88$, $P < 0.001$, $R^2_{adj} = 0.95$; LRT of GLMM: Xsq(1) = 95.558, P < 0.001, Table 4, Figure 3c).

Table 3

A generalized linear mixed effects model of the relatedness between an Ego and their Alters by rank

Term	Model 1	Model 2	Model 3
Intercept (male)	−0.073 (0.139)	0.473 (0.156)**	0.209 (0.162)
Gender (female)	−0.076 (0.105)	−0.063 (0.104)	−0.066 (0.103)
Age (standardized)	−0.080 (0.057)	−0.078 (0.057)	−0.082 (0.057)
Mum alive (no)	0.054 (0.176)	0.033 (0.175)	0.045 (0.175)
Dad alive (no)	−0.169 (0.108)	−0.177 (0.107)	−0.182 (0.106)
Number of genetic siblings	0.015 (0.019)	0.016 (0.019)	0.017 (0.019)
Offspring-binary (no)	0.085 (0.110)	0.105 (0.109)	0.097 (0.109)
In relationship (no)	0.243 (0.087)**	0.235 (0.087)**	1.061 (0.201)***
Rank		−0.231 (0.033)***	−0.124 (0.040)**
Rank × in relationship			−0.328 (0.068)***
Random effect covariances			
Subject intercept	4.030 (0.351)***	3.578 (0.318)***	3.481 (0.308)***
Intercept × slope (rank)	−1.341 (0.126)***	−1.141 (0.112)***	−1.097 (0.108)***
Subject slope (rank)	0.531 (0.052)***	0.441 (0.045)***	0.422 (0.044)***
Information criterion			
−2 log pseudo-likelihood	13042.645	12992.259	12979.711
Akaike corrected	13048.653	12998.268	12985.719
Bayesian	13066.487	13016.100	13003.551
Likelihood ratio test (df)	n/a	50.386 (1)***	12.548 (1)***
Number of observations (subjects)	2836 (540)	2836 (540)	2836 (540)

Degrees of freedom calculated with Satterthwaite approximation option.
Tests of fixed effects use robust covariances.
Likelihood ratio tests compare the change in −2 log pseudo-likelihood between nested models.
Relatedness modeled as a binomial-probit response variable from 0 to 0.5 in units of 0.125.
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 4

A generalized linear mixed effects model of the relatedness between an Ego and their related Alters by rank

Term	Model 1	Model 2	Model 3
Intercept (male)	1.555 (0.146)***	1.997 (0.155)***	1.979 (0.164)***
Gender (female)	−0.009 (0.114)	−0.062 (0.114)	−0.062 (0.113)
Age (standardized)	0.073 (0.071)	0.124 (0.067)	0.122 (0.067)
Mum alive (no)	0.293 (0.185)	0.278 (0.187)	0.281 (0.187)
Dad alive (no)	−0.318 (0.116)**	−0.369 (0.111)**	−0.369 (0.111)**
Number of genetic siblings	−0.001 (0.019)	0.004 (0.020)	0.004 (0.020)
Offspring-binary (no)	0.188 (0.138)	0.208 (0.130)	0.207 (0.131)
In relationship (no)	−0.177 (0.088)*	−0.268 (0.087)**	−0.232 (0.137)
Rank		−0.190 (0.017)***	−0.184 (0.025)***
Rank × in relationship			−0.013 (0.034)
Random effect covariances			
Subject intercept	0.172 (0.049)***	0.322 (0.051)***	0.319 (0.051)***
Intercept × slope (rank)	n/a	n/a	n/a
Subject slope (rank)	0.045 (0.007)***	0.009 (0.003)**	0.009 (0.003)**
Information criterion			
−2 log pseudo-likelihood	4510.009	4414.451	4418.326
Akaike corrected	4514.017	4418.460	4422.334
Bayesian	4524.535	4428.976	4432.849
Likelihood ratio test (df)	n/a	95.558 (1)***	−3.875 (1)
Number of observations (subjects)	1435 (497)	1435 (497)	1435 (497)

Degrees of freedom calculated with Satterthwaite approximation option.
Tests of fixed effects use robust covariances.
Likelihood ratio tests compare the change in −2 log pseudo-likelihood between nested models.
Relatedness modeled as a binomial-probit response variable from 0 to 0.5 in units of 0.125.
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

The main exception to this pattern was by respondents in a romantic relationship, as they often listed their romantic partner as their most likely person to seek support from (of 363 respondents in a relationship, 252 listed their partner, and 153 of these were in the top rank). This is shown by such respondents having a significantly lower intercept for relatedness by rank, and also a shallower slope by rank, leading to a significant interaction between relationship status and rank (LRT of GLMM: Xsq(1) = 12.548, $P < 0.001$, Table 2) that was not present when examining related alters only (LRT of GLMM: Xsq(1) = −3.875, $P = 1.000$, Table 3).

DISCUSSION

We found support for Hamilton's rule (Hamilton 1964) in Humans. Specifically, that 1) the average relatedness decreased with the likelihood of perceived support (Figure 3a); and 2) that individuals

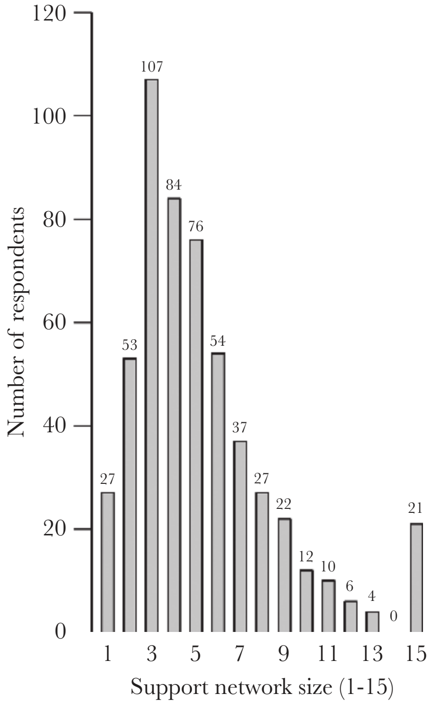

Figure 1
Frequency distribution of support network sizes, the sample sizes are shown above each column.

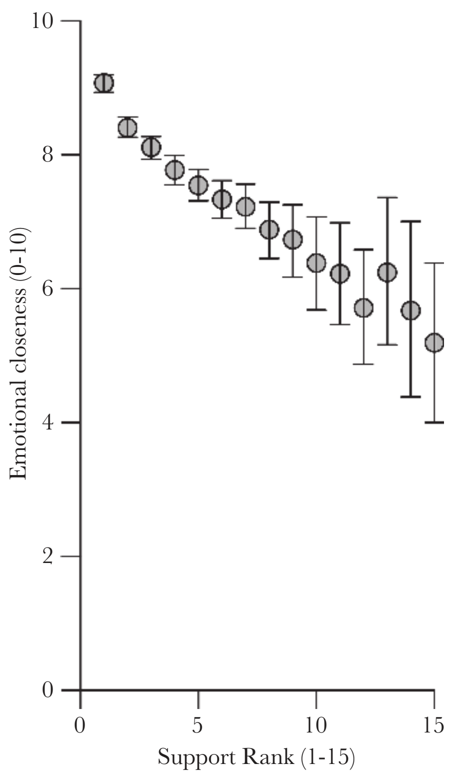

Figure 2
The relationship between an Ego's reported emotional closeness to an Alter and their ranking of that Alter by perceived likelihood of support during a severe emotional or financial crisis. Error bars are bootstrapped 95% confidence intervals.

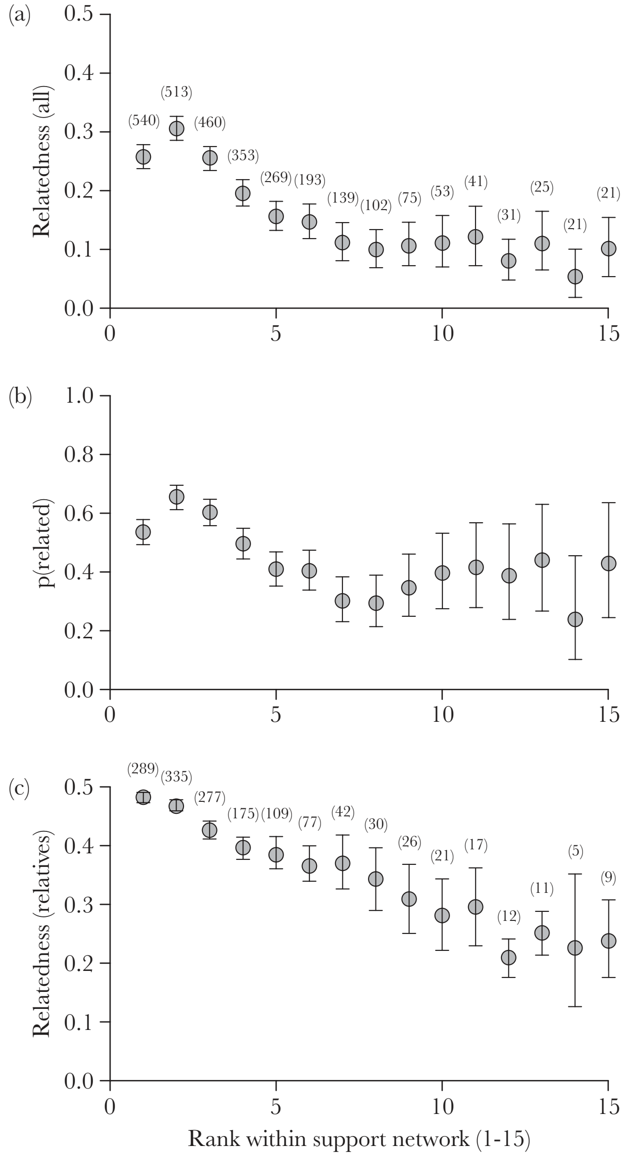

Figure 3
(a) Mean coefficient of estimated relatedness for Alters, (b) proportion of Alters that are related to Ego, and (c) mean coefficient of relatedness to Ego for related Alters only, plotted as a function of Ego's preferred ranking of Alters as a source of social and emotional support. Error bars are bootstrapped 95% confidence intervals.

felt they would more likely receive important support during a crisis from relatives and closer relatives than from distant relatives (Figure 3b,c). We also found that in general, emotional closeness, which has been shown to mediate the role of relatedness upon altruism (Korchmaros and Kenny 2001), predicts the perceived relative likelihood of receiving help (Figure 2).

For helping behaviors to be directed toward kin it is necessary to use some form of kin discrimination. Ideally, a genetic kin recognition system would be most accurate, but such a system is unlikely to be evolutionarily stable (Rousset and Roze 2007). This is because genetic kin recognition requires discrimination of a balanced genetic polymorphism, but also affects the evolution of such polymorphisms. Ultimately such a mechanism acts to erode the genetic variation necessary for its own effective function, through a process of positive feedback that favors the most common variants (Rousset and Roze 2007). Therefore it is expected that many organisms, including humans, use reliable cues from their environment, instead of genetic kin recognition, to infer kinship (Hamilton 1987). Examples of environmental cues reportedly used by humans are coresidence patterns when young and perinatal association with one's mother (Lieberman et al. 2007).

Psychologically, emotional closeness serves as a proximate mechanism to direct human affiliative behavior (Korchmaros and Kenny 2001), which is modulated by time spent together, but differently for friends compared to relatives (Roberts et al. 2008). Although people also report emotional closeness toward nongenetic relatives (Affines, e.g., an Ego's brother's wife), they do so in a manner consistent with inclusive-fitness theory and Fisher's reproductive value, that is, people do not need to be genetically related, it is enough to share a genetic interest in future offspring (Burton-Chellew and Dunbar 2011). It is therefore likely that people use cues of kinship, feelings of emotional closeness and expectations of reciprocity when differentiating among potential relationships (Osinski 2009; Neyer et al. 2011).

Emotional closeness in nonhumans is of course harder to measure, but the pattern of increased time spent together, measured via association or sociality indexes, being linked to increased support and fitness benefits is replicated in nonhuman primates (Silk 1994; Silk et al. 2003, 2010). This pattern is replicated for both kin and nonkin relations (Lehmann and Boesch 2009; Schülke et al. 2010).

Overall our results are consistent with other human network studies that analyzed patterns of self-reported actual help received, as opposed to our perceived future help if needed (Neyer and Lang 2003). Our results also replicate questionnaire-based studies that investigated the role of kinship and/or relatedness upon human cooperation (Essock-Vitale and Mcguire 1985; Kruger 2003; Webster 2003, 2008; Stewart-Williams 2007). For instance, Burnstein et al. (1994) used questionnaires to show that people understand differences in relatedness, are sensitive to differences in relatedness, and especially favor relatives when the hypothetical helping behavior concerns life-or-death situations. Korchmaros and Kenny (2006) also used hypothetical dilemmas to show that many factors, such as propinquity and frequency of interaction, mediate the relationship between genetic relatedness and willingness to help. Cues of kinship have also shown to have beneficial effects for group-level cooperation in experimental studies (Krupp et al. 2008).

One issue that we did not consider in our study is the scale of competition for our Egos (Hamilton 1971; West et al. 2006). When competition occurs locally (low scale of competition) altruism is less favored, which can happen when there is limited dispersal. The lack of dispersal increases competition among kin for material resources and mates, selecting against altruism despite limited dispersal increasing the average relatedness between actors (Taylor 1992). The interaction between relatedness and the scale of competition upon altruism has been shown in fig wasps (West et al. 2001), Nordic historical records (Dunbar et al. 1995), the Kipsigis agro-pastoralists of Kenya (Borgerhoff Mulder 2007), and in a matrilineal society in rural Malawi (Sear 2008). Ideally, we would have generated a covariate for the scale of competition, perhaps by asking our respondents to report their level of perceived competition with their relatives. However, one could argue that in today's free-mixing large-scale societies, with greater dispersal and more unrelated competitors, such kin competition is unlikely to be strong enough to select against altruism between relatives in general.

Many of our Alters were, of course, not genetically related to their Ego (49%) and therefore challenge Hamilton's rule. Although 14% of all Alters were actually romantic partners, who can increase their own direct fitness by helping the Ego, or the family of such partners (affinal kin) who may share a genetic interest in the offspring of such unions. It is therefore possible for their help to still satisfy Hamilton's rule (Hughes 1988, sections 4.3 and 5.2). This is because by increasing the reproductive success of one's affinal kin, one's "aid to consanguineal kin [can be] channeled through intermediaries" (Cronk 1991, p. 41), although the benefits are discounted by paternity uncertainty and the probability of divorce.

Genetic and affinal relatives aside, it remains that many of our Egos indicated a belief that nonrelatives would be willing to help them in a severe crisis. For such costly helping behavior to be evolutionarily stable, and to satisfy Hamilton's rule when $r = 0$, the costs to the actor must be directly recouped through mechanisms such as reciprocity (Trivers 1971). Therefore, our Egos would be predicted to be willing to reciprocate such help, although we did not test for this.

Mechanistically, many primates rely on kin for support, but they also rely on those that they have a relatively high sociality index with (i.e., "friends") to come to their aid during conflict (Kulik et al. 2012). Clearly the explanatory power of Hamilton's rule does not extend to these latter cases, nor to our data involving "friends." So whilst our data support Hamilton's rule, they do not rule out additional explanations for helping behavior. However, if Hamilton's rule was not important in explaining such helping behaviors, then while we may still see kin in the support network, we would not necessarily expect the correlation between likelihood of help and relatedness.

One caveat about our results is that as we failed to record the nationality of our respondents we are unable to automatically generalize these results cross-culturally, and we caution that our respondents are likely to be from western, educated, industrialized, rich democratic societies and thus to be WEIRD (sensu Henrich et al. 2010). However, we would speculate that the role of kinship is likely to be even larger in non-WEIRD respondents who live in smaller societies with less migration and emigration.

In summary, we found that, although 35% of ties within the support network were with neither relatives nor those that shared reproductive interests, close relatives were more likely to be ranked in primary positions, and that the degree of relatedness correlates with rank. This is evidence that, even though human social worlds contain extensive friendships and cooperation with nonrelatives, many of the important forms of social benefits are still provided in-line with the predictions of Hamilton's rule.

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