

SHORT COMMUNICATION

Assortative mating based on cooperativeness and generosity

A. TOGNETTI*†, C. BERTICAT*†, M. RAYMOND*† & C. FAURIE*†

*University of Montpellier 2, Montpellier, France

†CNRS, Institute of Evolutionary Sciences, Montpellier, France

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Cooperative behaviour and generosity towards nonkin represent costly and risky behaviour that could be used as a signal of mate quality. Therefore, cooperative traits could serve as criteria in mate choice, leading to assortative mating for those traits. There is evidence of similarity in couples for altruistic traits. However, the literature is based on self-reports and does not provide conclusive proof of either a convergence across time or mating preferences. Here, we report a field experiment, conducted in rural villages in Senegal, showing that husbands and wives are similar with respect to their contributions to a public good and their charity donations. Further analyses suggest that this similarity is due to initial assortment rather than convergence of phenotypes.

Introduction

In humans, assortative mating has been found for a high number of traits, including socio-economic, educational, psychological and physical traits (e.g. Stevens *et al.*, 1990; Berezkei *et al.*, 2002; Silventoinen *et al.*, 2003; Little *et al.*, 2006). However, few studies have examined whether it also occurs for altruistic behaviour, and all of them were based on self-ratings. Therefore, the existence of mating preferences for cooperative traits has never been clearly and experimentally established in studies of real couples.

Experimental measures reflecting components of altruism are shown to be heritable, such as the amount invested and reciprocated in the trust game (Cesarini *et al.*, 2008) and the responder's behaviour in the ultimatum game (Wallace *et al.*, 2007). Moreover, a significant association was found between the voluntary contribution in a public good game (PGG) and the polymorphism of the monoamine oxidase A gene, suggesting that it is partly genetically determined (Mertins *et al.*, 2011). It is therefore likely that the contributions in a PGG and other components of altruistic behaviour

are heritable, which is a necessary condition for those traits to evolve through selection.

Individuals may behave altruistically for reputation reasons because selective benefits (associated with status) accrue to the generous (competitive altruism hypothesis: Roberts, 1998). Experimental studies show that if contributions are public, people are more altruistic (Rege & Telle, 2004; Hardy & Van Vugt, 2006), and the most altruistic participants gain the highest status and are most frequently preferred as interaction partners (Sylwester & Roberts, 2010; Barclay, 2011). At university, prosocial students tend to select other prosocial students to play a social dilemma game (Sheldon *et al.*, 2000).

The benefits of having a reputation of cooperator may include increased reproductive success. Indeed, experiments showed that men contribute more to public goods in the presence of women, that their contributions significantly increase over time and that they volunteer more for charitable causes (Tognetti *et al.*, 2012; Van Vugt & Iredale, 2013), supporting the idea that men compete with each other by cooperating to impress women.

Cooperation can therefore be used as a cue that other individuals can use to make social decisions, either to select partners to cooperate with or to select sexual partners (Miller, 2007; Nesse, 2007). In addition, if cooperative behaviour is socially and/or sexually selected, cues for the propensity to cooperate can evolve into signals. Cues are nonselected ways of obtaining information, whereas a signal is defined as any act which alters the

Correspondence: Arnaud Tognetti and Charlotte Faurie, Université Montpellier 2, Pl. E. Bataillon, CC065, 34095 Montpellier, France. Tel.: +33 4 67 14 46 32; fax: +33 4 67 14 36 22; e-mails: arnaud.tognetti@gmail.com and charlotte.faurie@univ-montp2.fr

behaviour of others, evolved because of that effect, and is effective because the receiver's response has also evolved (Maynard-Smith & Harper, 2003).

One of the main mechanisms hypothesized to ensure the honesty of a signal is condition dependence; signals have to be costly so that only high-quality individuals can support the cost of exhibiting them (Zahavi, 1977). Altruistic acts represent costly behaviour (Heinsohn & Legge, 1999). They could therefore signal the individual's quality (theory of costly signalling; Zahavi, 1995; Roberts, 1998), which can be transmitted to offspring. Such a signal can be used in mate choice. Alternatively (and nonexclusively), cooperativeness towards nonkin may be a signal of the propensity to engage in other cooperative actions, such as child care and provisioning (Miller, 2007; Tognetti *et al.*, 2012). Because parental investment (from both parents) is a crucial resource for human children (Sear & Mace, 2008), reproduction with a cooperative mate who invests in offspring is likely to be an adaptive strategy.

Consequently, preferences for altruistic traits could have evolved, and potentially have led to assortation. There is some evidence of assortation according to cooperativeness outside mate choice. At school, altruists are friends with more altruistic classmates than are egoists (Pradel *et al.*, 2009). Even chimpanzee friendships are based on homophily in personality (Massen & Koski, 2013). Concerning mates, several studies have shown that spouses have similar values of altruistic traits, but the literature is unclear on whether this similarity is due to preferences. Indeed, some suggested that psychological traits converged after marriage (e.g. Guttman & Zohar, 1987; Keller *et al.*, 1995; Little *et al.*, 2006), whereas others showed that similarity did not increase with time spent together (Watson *et al.*, 2004; Luo & Klohnen, 2005). Moreover, these results are based on self-ratings of altruism using questionnaires in Western societies, and the literature lacks both experimental measures and non-Western studies.

To fill these gaps, we conducted an experimental study to assess cooperativeness and generosity in a sample of men and women in rural Senegal. Cooperativeness was measured in a PGG, and generosity was measured in a task involving charitable contributions. Marital status and time since marriage were collected to examine whether spouses were similar on both of these altruistic measures and to investigate whether this similarity was the result of convergence across time or of initial assortment due to preferences.

Materials and Methods

Population

This study was conducted in Senegal (Sine Saloum). We recruited 156 men and 172 women, from five

villages of approximately 300 inhabitants. Among these participants, there were 51 married men whose wife (first wife when polygynous) was present in the sample. In this population, men in a village are often genetically related and a neighbourhood is generally constituted of a man's and his sons' households. However, due to female-biased dispersal in this population, married women are generally not related, and in a couple, the husband and the wife are not related either. For each participant, information was collected on their age, marital status, number of children, weight, height and socio-economic status (cattle and land possessions were weighted by their average price). Written informed consent was obtained from all subjects.

Measures of cooperativeness

In each session, groups of four men, or four women, were invited to participate in a PGG. To avoid close kinship between participants, the four members of a group were from different neighbourhoods. They were neither told the aim of the experiment nor that it would be followed by an invitation to make a donation. At the beginning of each session, the instructions for the game were thoroughly explained by a local research assistant in the native language of the participants. Decision-making took place inside a van, so that group members and other villagers could not observe the participant.

The PGG

We adapted the PGG rules to field conditions. A session included five periods (sequential game), thereby including aspects of reciprocity in our evaluation of cooperation. In each period, each of the participants received 200 g of rice (we used rice instead of coins to obtain continuous data and because most participants were illiterate, making calculations and conversions problematic). The four same-sex participants entered a van one by one and divided their endowment between a private and a public good, represented by opaque boxes (anonymity of allocations). At the end of each period, they were informed about the total amount placed by the group in the public box during this period. After the game, the amount of rice in the public box was doubled and divided in four equal gains among the four group members, to which their private box was added. Thus, all players received an equal share of the accumulations in the collective good irrespective of their contributions. The proportion of their endowment allocated in the public good was considered as a measure of their cooperative inclinations.

The donation test

When the players individually received their final payoff in the van, they were informed of the possibility of donating part of it to the school's canteen. It was

specified that this donation was optional and that any amount of rice would be accepted. Each participant left the van with an opaque bag containing the payoff won during the game minus the donation, if any. Note that in each of the villages selected for this study, there was one (and only one) school, so that all school age children attended this school.

Statistical analyses

Similarity of cooperativeness in the PGG

To investigate whether husbands and wives behave similarly in the PGG, two kinds of variables were investigated: the amount invested in the public box in the first period (P_1), representing spontaneous contribution (before knowing how other members of the group played), and the average contributions over the five periods of the game (P_1P_5), representing global cooperativeness. First, Spearman's rank correlation tests were performed to examine whether husband's cooperativeness and wife's cooperativeness were correlated. Then, to control for the fact that spouses live in the same village, linear mixed models were performed both for P_1 and P_1P_5 . Husbands' cooperativeness was used as the response variable, their wives' cooperativeness as an explanatory variable, and village as a random effect.

In addition, we used linear models, the response variable being the absolute difference in spouses' amounts invested in the public box (both for P_1 and P_1P_5), in order to test whether similarities between spouses were linked to the duration of exposure to each other (time since marriage) or to age similarity. A square-root transformation of the response variable was used when necessary to normalize the residuals. We also tested various nonlinear potential effects of time since marriage (squared, inverse, logarithmic, exponential or square-root transformations).

Similarity of generosity in the donation test

Spearman's rank correlation tests were used to examine the link between husband's and wife's proportion of their PGG gain donated to the school. Then, generalized linear mixed models (fitted with a binomial error structure) were used to control for a potential confounding village effect. Husbands' proportion of gain donated was used as a response variable, their wives' proportion donated as an explanatory variable and, village as a random effect.

Moreover, generalized linear models with the similarity of generosity between spouses as the response variable were used to test the potential effect of the duration of spouses' exposure and of the age similarity. Due to the high proportion of individuals who did not make a donation (13 men and 17 women of 51 couples), the analyses were split into two types of models: (i) the response representing behavioural similarity

between spouses was fitted with a binary error structure (1 when both donated or both did not donate, 0 otherwise), and (ii) when at least one spouse made a donation, the absolute difference between the spouses, in their proportion of their gain donated, was fitted with a Gaussian error structure. Square-root transformations were used when necessary to normalize the residuals. Finally, various nonlinear potential effects of time since marriage were investigated (squared, inverse, logarithmic, exponential or square-root transformations).

Results

The 102 individuals composing the couples included in the present study did not differ from the other 226 participants (who were either married to a nonparticipant or single) in terms of either their average contributions over the five periods of the PGG (couples: 109 ± 34 g, others: 111 ± 41 g, Wilcoxon test: $W = 9953$, $P = 0.55$) or their donations (couples: 121 ± 129 g, others: 107 ± 119 g, $W = 11665$, $P = 0.34$). In this study sample (and in the whole sample), no sex difference was found for the average contributions over the five periods (men: 108 ± 37 g, women: 111 ± 31 g, $W = 1101$, $P = 0.48$) or the donations (men: 126 ± 139 g, women: 116 ± 119 g, $W = 1321$, $P = 0.75$). Similarly, no effect of age, socio-economic status, weight, height, number of years of school attendance or number of children was found with the average contributions over the five periods (Spearman's rank test, all $-0.17 > \rho > 0.20$, and $P > 0.17$) or with the amount donated (all $-0.26 > \rho > 0.08$, and $P > 0.07$). The average age was 50 ± 13 for men and 37 ± 12 for women. The average number of children was 6 ± 2 for men and 5 ± 3 for women. Given the average mother's age, the average numbers of children and the fact that children go to school between 6 and 12 years old, it is likely that most parents had at least one child in the village school. The variances in contributions in the PGG were not different between individuals who had attended school and individuals who had not (men: $F_{34,13} = 0.95$, $P = 0.85$; women: $F_{44,3} = 0.57$, $P = 0.34$), ensuring that participants generally understood the game's rules correctly.

Finally, no correlation was observed between contributions (either P_1 or P_1P_5) and donations (Spearman's rank test, all $-0.17 > \rho > 0.08$; $P > 0.25$), nor between final payoff in the PGG and the amount or proportion given to the school (all $-0.17 > \rho > 0.05$; $P > 0.22$) (as in the total sample, see Tognetti *et al.*, 2012). This suggests that our two measures do not represent the same component of cooperative behaviour.

Due to missing information, a few couples were excluded from the following analyses (four couples for the PGG and one for the donations).

Assortative mating based on cooperativeness and generosity

We found a positive correlation between husbands' and wives' contributions in the PGG, both in P_1 ($\rho = 0.28$, $P = 0.05$) and P_1P_5 ($\rho = 0.51$, $P = 0.0002$; Fig. 1a,b). Similarly, the proportions of the gain donated were positively correlated between husband and wife ($\rho = 0.36$, $P = 0.01$; Fig. 2a). These links remained positive when controlling for a potential village effect both for the contributions (P_1 : $F_{1,44} = 3.52$, $P = 0.07$; P_1P_5 : $F_{1,41} = 14.05$, $P = 0.0005$) and the proportion donated ($\chi^2 = 5.39$, d.f. = 1, $P = 0.02$).

Nevertheless, although these results indicate a significant positive link between husbands' and wives' proportion of gain donated, this link is not as obvious in the Fig. 2 as in the Fig. 1a,b. This is partly explained by the overrepresentation of couples among which both spouses did not donate ($n = 9$; Fig. 2b). The correlation is not found anymore when these couples are excluded from the analysis ($\rho = 0.03$, $P = 0.85$), suggesting that similarity lies in the fact that one did donate or not, but not in the amount donated. This view is supported by the result of a binomial exact test, which indicated that the probability that both spouses behaved similarly – both donated ($n = 29$ couples) or both did not donate ($n = 9$ couples) – was significantly higher than chance expectations (proportion of couples behaving similarly: 76%, $P < 0.001$).

Effect of the time of exposure and age similarity

No influence of the time since marriage on similarity between spouses was detected, either in the PGG (P_1 :

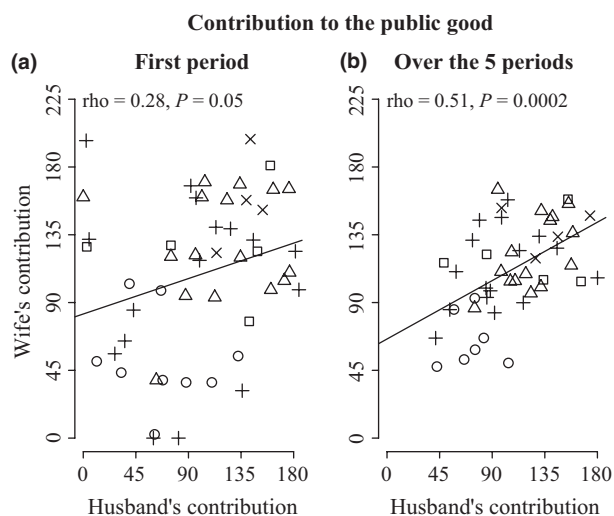


Fig. 1 Couples contribution to the public good (raw data in grams of rice). symbols represent membership in different villages. Lines indicate the relationship between husbands' and wives' contributions. Spearman's rank tests revealed a positive correlation for contributions in the public good game.

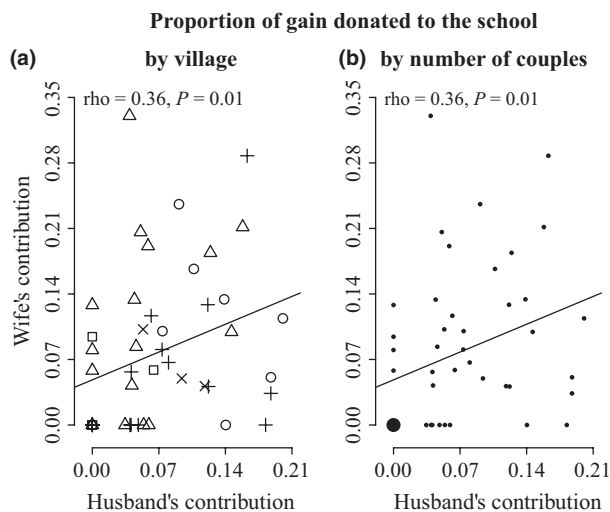


Fig. 2 Couples proportion of gain donated to the school canteen (raw data in grams of rice). (a) Symbols represent membership in different villages. (b) The surface of the data points is proportional to the number of couples. Lines indicate the relationship between husbands' and wives' contributions. Spearman's rank tests revealed a positive correlation. Although a positive correlation was found between husbands' and wives' proportions of gain donated, this effect seems partly explained by the overrepresentation of couples among which both spouses did not donate ($n = 9$). The result of a binomial exact test indicated that the probability that both spouses behaved similarly (both donated or both did not donate) was significantly higher than chance (probability of behaving similarly: 76%, $P < 0.001$).

$\beta = 0.02$, $F_{1,48} = 0.39$, $P = 0.53$; P_1P_5 : $\beta = 0.01$, $F_{1,45} = 0.22$, $P = 0.64$) or in the donation (behavioural similarity: $\beta = -0.04$, $\chi^2 = 1.43$, d.f. = 1, $P = 0.23$; proportion of gain donated: $\beta = -0.001$, $F_{1,37} = 0.82$, $P = 0.37$). Neither was there any effect of age similarity both for the PGG (P_1 : $F_{1,47} = 3.42$, $P = 0.07$; P_1P_5 : $F_{1,45} = 0.41$, $P = 0.52$) and the donation (behavioural similarity: $\chi^2 = 0.73$, d.f. = 1, $P = 0.39$; proportion of gain donated: $F_{1,36} = 2.90$, $P = 0.10$). None of the various nonlinear effects of the variable time since marriage tested was significant (results available upon request).

Discussion

In our experiment, based on contributions to a public good and charitable donations, men's and women's altruism in Senegalese villages were independently assessed. We found that, in both tasks, spouses behave in the same way. Moreover, this result was maintained when controlling for the membership in a same village, and it was independent of time since marriage or age similarity. This suggests the existence of mate preferences based on cooperativeness and generosity in this culture.

The preference for a cooperative partner could result from several causes: (i) because of the cost involved, cooperative skills could constitute a signal of mate quality; (ii) because parental investment is a form of cooperative breeding, cooperative skills could constitute a signal of parent quality; (iii) because reciprocal helping and collective actions are particularly frequent and crucial for survival in rural communities (e.g. building a house, digging a well, resource provisioning), having a spouse with a good reputation of cooperator is likely to be beneficial in several contexts.

Selection for homogamy could be based on kin selection, because homogamy translates into higher parental-offspring relatedness (genetic similarity theory: Rushton, 1989). Alternatively, it could reflect outbreeding avoidance. Indeed, outbreeding induces a loss in fitness in several species (Keller & Waller, 2002) including humans (e.g. Postma *et al.*, 2010). Consequently, there should be an optimal balance between inbreeding and outbreeding (Bateson, 1978; Roberts & Little, 2008). Consistent with this, there is apparently an optimal relatedness between spouses in humans (Helgason *et al.*, 2008). Both kin selection and outbreeding avoidance are more likely to rely on traits that are primarily genetic, such as physical traits, which however appear to be partly correlated with cooperativeness (Stirrat & Perrett, 2010). Selection for homogamy could also be based on nongenetic, but fitness-maximizing, mechanisms. Similar spouses may get along more easily with each other, as indicated by studies showing that friends have similar personalities (McPherson *et al.*, 2001) and that trust is enhanced by resemblance (DeBruine, 2002). As a consequence, similar spouses may reproduce more successfully and provide better parental investment. Moreover, there could be attrition of dissimilar pairs due to separation.

Mate similarity can also occur as a side effect of competition for mates, even though all individuals prefer mates belonging to the same category (Miller & Todd, 1998): attractive individuals (altruists) can pick their preferred mate from the available pool, leaving unattractive (selfish) individuals to pair with those that remain unpaired. Nevertheless, marriage decisions do not always reflect mates' preferences. In rural Senegal, parents traditionally had an influence: they most often forbid a marriage across different casts (e.g. nobles, griots or blacksmiths), but men and women were free to choose their partner within a cast, and cast endogamy has lost importance over the last few decades. Note that the parents may display homogamous preferences for their offspring, for the same evolutionary reasons mentioned above.

Several potentially confounding phenomena can however explain homogamy. First, even if similarity is based on assortment at the time of meeting, it is not necessarily due to active preferences. People who are

similar in personality, interests or backgrounds may be more likely to meet each other. For example, if mate choice occurs within socio-economic classes (Drìbe & Lundh, 2009), it will automatically generate homogamy for traits that are specific to each class. Cooperativeness is indeed distributed differently across social classes in the United Kingdom (Nettle *et al.*, 2011), but in our sample, we found no relationship between socio-economic status, contributions to public goods and charity donations. Moreover, there is no correlation between a husband and his wife concerning the number of years of school attended ($\rho = 0.17$, $P = 0.23$) and therefore no evidence of assortative mating over education in this sample.

Second, spouses' phenotypes may be similar because they have converged across time. In our sample, however, we did not find a significant effect of the time since marriage on similarity. This result suggests preferences at the time of couple formation rather than convergence. Nevertheless, the couples in this sample have been married on average for 21 years, ranging from 3.5 to 42.5 years: we were not able to test the effect of time since marriage in the first 3.5 years, and the possibility that behaviour rapidly converged after marriage cannot be excluded. However, among studies showing an effect of the time spent together, none found evidence that psychological traits converge rapidly after marriage; actually, it seems to be a slow process instead (e.g. Guttman & Zohar, 1987; Keller *et al.*, 1995; Little *et al.*, 2006). Finally, several studies showed evidences for an absence of convergence (Watson *et al.*, 2004), including one with a large sample of newlyweds (range 25–452 days; Luo & Klohnen, 2005). Therefore, it seems unlikely that the similarity observed in our population is due to a rapid convergence occurring in the first months.

Preferences for a cooperatively similar mate constitute a possible mechanism for the evolution of altruism among nonkin. Indeed, such preferences can lead to the evolution of altruism if the advantage of egoistic individuals is outcompeted by the benefits of mutual cooperation between altruists. This selection requires that (i) altruists can easily be distinguished from egoists, (ii) altruists mate with altruists, leaving egoists no choice but to mate with each other. Therefore, it is probable that the ability to quickly detect whether an individual is altruistic or not from physical features will be positively selected. Indeed, several studies showed that facial traits could be used as a signal of cooperativeness, such as emotional expressivity (e.g. Oda *et al.*, 2009) and male static facial traits (Stirrat & Perrett, 2010; Tognetti *et al.*, 2013). Our study therefore provides support for the idea that homogamy has been involved in the evolution of human cooperation. It remains to be established whether these results can be confirmed in other cultures.

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