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## **A threshold for biological altruism in public goods games played in groups including kin**

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**Abstract:** Phenomena like meat sharing in hunter-gatherers, altruistic self-sacrifice in intergroup conflicts, and contribution to the production of public goods in laboratory experiments have led to the development of numerous theories trying to explain human prosocial preferences and behavior. Many of these focus on direct and indirect reciprocity, assortment, or (cultural) group selection. Here, I investigate analytically how genetic relatedness changes the incentive structure of that paradigmatic game which is conventionally used to model and experimentally investigate collective action problems: the public goods game. Using data on contemporary hunter-gatherer societies I then estimate a threshold value determining when biological altruism turns into maximizing inclusive fitness in this game. I find that, on average, contributing no less than about 40% of individual fitness to public goods production still is an optimal strategy from an inclusive fitness perspective under plausible socio-ecological conditions.

**JEL:** B15, C72, D64, H41

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## 1. Introduction

The high levels of cooperativeness and altruism observed in humans have been a prominent subject of economic, psychological, and anthropological research in the last decades (West, Griffin, and Gardner 2007a; Nowak 2012). Phenomena like meat sharing in hunter-gatherers (Hawkes 1993; Hill 2002), altruistic self-sacrifice in intergroup conflicts (Choi and Bowles 2007; Rusch 2013), and contribution to the production of public goods in economic laboratory experiments (Fehr and Gächter 2002; Chaudhuri 2011) have led to the development of numerous theories trying to explain human prosocial preferences and behavior. Few of the more recent theories in this field, however, have paid explicit attention to the biologically utmost relevant factor of relatedness (Boyd, Schonmann, and Vicente 2014). Instead, they focus on direct and indirect reciprocity, assortment, or (cultural) group selection (Nowak 2006). Here, I investigate analytically how kinship changes the incentive structure in that paradigmatic game which is conventionally used to model and to experimentally investigate collective action problems: the public goods game. I then use recent field data from contemporary hunter-gatherer societies to estimate the upper bound of a threshold value determining when biological altruism turns into maximizing inclusive fitness in this game. It turns out that, on average, contributing no less than about 40% of individual fitness to public goods production still is an optimal strategy from an inclusive fitness perspective.

Supposing that the field data used to calibrate here provide a good estimate of the conditions under which the relevant human psychological mechanisms for public goods provision evolved, this result might add substantially to the explanation of why we observe positive contributions in public goods games so frequently.

## 2. Public goods games in groups including kin

In the conventional  $n$ -player one-shot linear public goods game, PGG, where each player can contribute an amount of  $c_i \geq 0$ , an individual player's payoff is given as

$$\pi_i(c_i) = \frac{m}{n} \sum_{j=1}^n c_j - c_i.$$

This means: All players' contributions are multiplied by a constant  $m > 1$ , added up, and then equally redistributed among all players. Deriving this expression with respect to  $c_i$  yields that  $\pi_i(c_i)$  will increase in  $c_i$  whenever  $m/n > 1$ , i.e., whenever the marginal per capita return,  $m/n \equiv b$  (MPCR), on investment is greater than one; for  $m = n$ , every contribution  $c_i$  is an equilibrium strategy; else, the optimal strategy in this game is not to invest at all, i.e.,  $c_i = 0$ . Now, interpret this game in terms of fitness, i.e., let  $\pi_i$  and  $c_i$  denote expected numbers of copies of a gene which will be transferred to the next generation and assume that some of the players can be related (van Veelen 2009; Ohtsuki 2014). Using the conventional

coefficient of relatedness,  $r_{ij}$ , denoting the expected fraction of genes shared by player  $i$  and player  $j$ , this turns the PGG into the following kinship public goods game, ‘k-PGG’:

$$\Pi_i(c_i) = \sum_{j=1}^n r_{ij} \left( b \sum_{j=1}^n c_j \right) - \sum_{j=1}^n r_{ij} c_j$$

where  $r_{ii} = 1$ . This means: In addition to the direct benefit which player  $i$  derives from his share of the public good, he also indirectly benefits from the shares of the public good which his relatives receive weighted by the respective relatedness coefficients, but, of course, he also shares the respective parts of their costs. Deriving this expression with respect to  $c_i$  yields that  $\Pi_i(c_i)$  increases with  $c_i$  whenever  $b \sum_{j=1}^n r_{ij} > 1$ , i.e., when the MPCR times the  $i$ -th row sum of the relatedness matrix  $r_{ij}$ , i.e., the expected marginal per gene return, is greater than one. (Note that if we assume only one related individual in the group this reduces to Hamilton’s inequality Hamilton 1964). We can use this expression to derive specific thresholds,  $\theta_i$ , for the MPCR of the k-PGG for a given individual  $i$ : Individual investment, i.e.,  $c_i > 0$ , in this game is optimal whenever

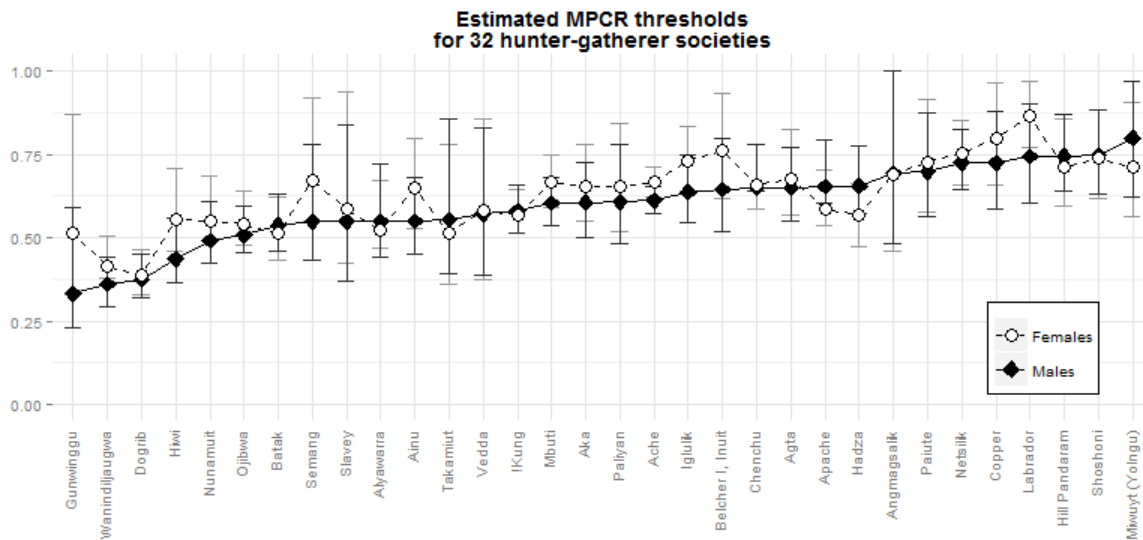
$$\frac{m}{n} > \left( \sum_{j=1}^n r_{ij} \right)^{-1} \equiv \theta.$$

For comparison: in the PGG without relatives  $\theta \equiv 1$  for all individuals implying  $m > n$  as the condition for investing to be optimal.

### 3. Estimates of $\theta$ for 32 contemporary hunter-gatherer societies

Thanks to the invaluable data collection efforts by Kim Hill and colleagues (Hill et al. 2011), we can use this calculation to directly estimate  $\theta$  for average male and female target individuals in 32 contemporary foraging societies. This source provides detailed data on co-residence patterns in hunter-gatherer groups. These are conventionally assumed to be the best available model populations for the social structures in which we lived throughout most of our species’ history (95%, Hill et al. 2011). It is frequently argued that it is this social ‘environment of evolutionary adaptedness’ (‘EEA’, Cosmides and Tooby 2003) that should be taken into account when trying to explain the ultimate functions of human behavioral traits. While this view has been substantially criticized, numerous studies have found quite robust evidence that humans, at least in the statistical average, do react adaptively to a number of evolutionarily relevant ecological conditions (Volland 1998; Dunbar and Barrett 2009; Laland and Brown 2011). So let us assume, for now, that (i) the kinship structures reported by Hill and colleagues are representative of our social EEA and (ii) that they exerted an influence on the evolution of the cognitive mechanisms we deploy when making investment decisions in real-world and maybe even in laboratory PGGs.

Hill et al. report data on the average numbers of primary kin residing in the same group like male and female target individuals, i.e., on their average numbers of parents, siblings, and children present. The conventional relationship coefficient for all primary kin is  $r = 0.5$ . (In human groups as small as the ones in this sample, relatedness might even be higher due to inbreeding effects.) As Hill et al. do not report data on age of primary kin, I will only use the average number of siblings,  $s$ , and the average number of offspring,  $o$ , to estimate  $\theta$ , i.e., only the number of those primary kin who are likely to be reproductive still. Including parents in the calculation yields lower values of  $\theta$ , see Table S1 and Figure S1 in the Supplementary Materials below. The estimates presented in the following therefore represent conservative upper bounds. Using  $s$  and  $o$  we can calculate  $\theta = (1 + 0.5 [s + o])^{-1}$ . (The four missing data points in Hill et al.’ original data,  $n = 508$ , are assumed to be zero to receive the most conservative estimate.) For the 32 societies censused the calculation yields average  $\theta$ s of 0.63 ( $\pm 0.11$  sd.) for female target individuals and of 0.60 ( $\pm 0.11$  sd.) for males. The individual estimates are displayed in Fig. 1 and listed in Table S1. The slightly higher values for females are due to the fact that a majority of the societies in this sample reside patrilocally (15, matrilocally: 5, unknown/ambiguous: 12).



**Fig. 1:** Estimated threshold values for the minimum marginal per capita return required to make investing in the provision of linear public goods an optimal strategy in the presence of reproductive primary kin (siblings and own offspring) for the 32 hunter-gatherer societies censused by Hill et al. 2011; separate lines for male and female target individuals; sorted increasingly, left to right, by thresholds for male targets; error bars show upper and lower estimates based on the 95% confidence intervals reported by Hill et al..

In all 32 societies surveyed the conservative threshold estimates for the minimum MPCR required to make investing in the provisioning of public goods in the presence of kin an optimal strategy are thus

remarkably smaller than one, which is the benchmark MPCR value that should rule rational decision making in one-shot PGGs with no kin present. On average, only roughly 60% of fitness invested need to be returned directly to the investor. The indirect benefits induced by kinship structure suffice to compensate him or her for the gross loss of the other 40%. This analysis shows that before labelling public goods provisioning ‘altruistic’ in the biological meaning of the term (West, Griffin, and Gardner 2007b; West, El Mouden, and Gardner 2011), i.e., interpreting costs and benefits in terms of fitness, kinship structure must be taken into account, as it can substantially lower the MPCR threshold required for contributing to become optimal from an inclusive fitness perspective.

For the forgoing calculation I have assumed that contribution levels are unconditional strategies and shown that positive contributions can maximize inclusive fitness given a sufficiently high MPCR. Laboratory experiments using photos manipulated to include subtle kinship cues, however, repeatedly found that subjects can condition choices on these cues when facing stylized cooperation problems (DeBruine 2002, 2005; Krupp et al. 2012). Moreover, it is probably safe to assume that under ancestral conditions humans will have had quite reliable impressions of the number of kin they were interacting with, of the total size of their current group, and of the payoffs of specific public goods. The availability of this information allows for more differentiated conditional strategies to evolve than assumed here.

Furthermore, unlike other explanations for public goods provision under ancestral conditions (Choi and Bowles 2007), the k-PGG model presented here does not require any form of intergroup interaction in order to explain why we might observe positive amounts of individual fitness being invested for the benefit of the own group. From an inclusive fitness perspective, such a behavior is optimal as long as sufficient numbers of kin are present and benefit enough from the public goods produced. The estimates presented here indicate that this was quite likely the case during most of human evolution.

### **Acknowledgments**

All data on residence patterns used in this paper are available in the online Supporting Information to Hill et al., 2011, *Science* 331(6022): pp. 1286-1289 (doi: 10.1126/science.1199071). I thank Max Albert, Matthias Greiff, and Eckart Voland for valuable discussions.

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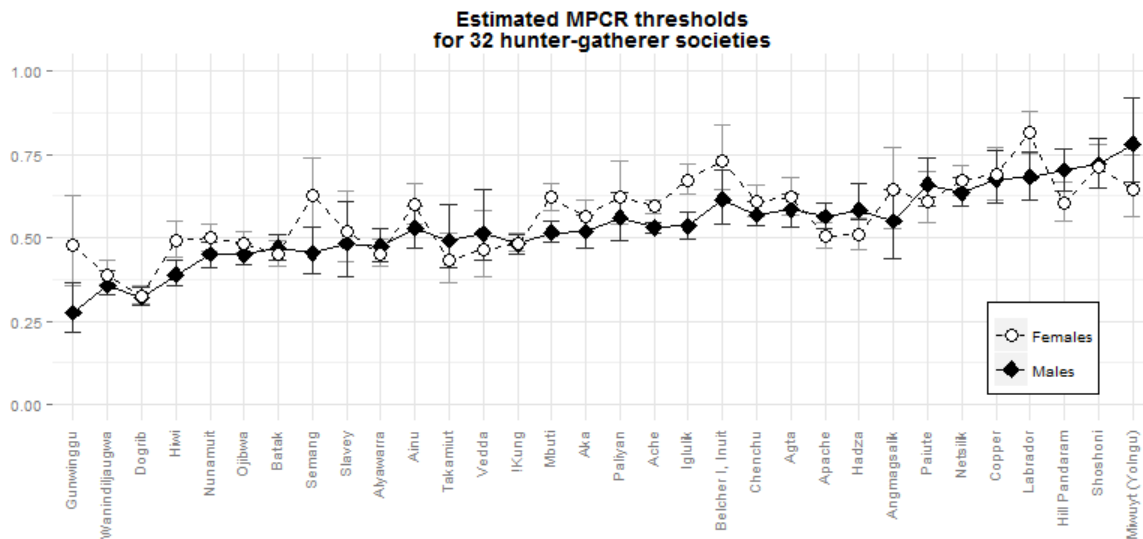
**Supplementary Materials**

<b>Society</b>	<b>Teta (reprod. primary kin)</b>		<b>Teta (total primary kin)</b>	
	<b>Females</b>	<b>Males</b>	<b>Females</b>	<b>Males</b>
Gunwinggu	0.51 (0.87-0.33)	0.33 (0.59-0.23)	0.48 (0.63-0.36)	0.28 (0.36-0.22)
Labrador	0.87 (0.97-0.77)	0.74 (0.9-0.6)	0.82 (0.88-0.75)	0.68 (0.76-0.61)
Semang	0.67 (0.92-0.55)	0.55 (0.78-0.43)	0.63 (0.74-0.53)	0.45 (0.53-0.39)
Iglulik	0.73 (0.83-0.64)	0.64 (0.75-0.55)	0.67 (0.72-0.63)	0.53 (0.58-0.5)
Belcher I. Inuit	0.76 (0.93-0.62)	0.65 (0.8-0.52)	0.73 (0.84-0.65)	0.62 (0.7-0.54)
Mbuti	0.67 (0.75-0.59)	0.60 (0.68-0.54)	0.62 (0.66-0.58)	0.52 (0.55-0.49)
Hiwi	0.55 (0.71-0.46)	0.44 (0.56-0.36)	0.49 (0.55-0.44)	0.39 (0.43-0.36)
Angmagsalik	0.69 (1-0.46)	0.69 (1-0.48)	0.65 (0.77-0.53)	0.55 (0.64-0.44)
Ainu	0.65 (0.8-0.53)	0.55 (0.68-0.45)	0.60 (0.66-0.54)	0.53 (0.59-0.47)
Ache	0.67 (0.71-0.62)	0.61 (0.66-0.57)	0.60 (0.61-0.57)	0.53 (0.55-0.51)
Paliyan	0.66 (0.84-0.52)	0.61 (0.78-0.48)	0.62 (0.73-0.54)	0.56 (0.64-0.49)
Nunamuit	0.55 (0.68-0.49)	0.49 (0.61-0.42)	0.50 (0.54-0.46)	0.45 (0.49-0.41)
Aka	0.65 (0.78-0.55)	0.61 (0.73-0.5)	0.56 (0.62-0.52)	0.52 (0.57-0.47)
Chenchu	0.66 (0.78-0.59)	0.65 (0.78-0.64)	0.61 (0.66-0.56)	0.57 (0.61-0.53)
Netsilik	0.75 (0.85-0.66)	0.72 (0.82-0.65)	0.67 (0.72-0.63)	0.63 (0.68-0.6)
Agta	0.68 (0.82-0.57)	0.65 (0.77-0.55)	0.62 (0.68-0.57)	0.58 (0.63-0.53)
Slavey	0.59 (0.94-0.42)	0.55 (0.84-0.37)	0.52 (0.64-0.43)	0.48 (0.61-0.38)
Ojibwa	0.54 (0.64-0.48)	0.51 (0.6-0.45)	0.48 (0.52-0.45)	0.45 (0.48-0.42)
Wanindiljaugwa	0.41 (0.5-0.38)	0.36 (0.44-0.29)	0.39 (0.43-0.36)	0.36 (0.4-0.33)
Copper	0.80 (0.97-0.66)	0.72 (0.88-0.59)	0.69 (0.77-0.61)	0.68 (0.76-0.61)
Dogrib	0.39 (0.46-0.33)	0.38 (0.45-0.32)	0.33 (0.36-0.3)	0.32 (0.35-0.3)
!Kung	0.57 (0.64-0.51)	0.58 (0.66-0.51)	0.48 (0.52-0.46)	0.48 (0.51-0.45)
Shoshoni	0.74 (0.88-0.62)	0.75 (0.88-0.63)	0.71 (0.78-0.65)	0.72 (0.8-0.65)
Batak	0.51 (0.62-0.43)	0.54 (0.63-0.46)	0.45 (0.49-0.41)	0.47 (0.51-0.43)
Alyawarra	0.52 (0.67-0.47)	0.55 (0.72-0.44)	0.45 (0.5-0.41)	0.48 (0.53-0.43)
Vedda	0.58	0.57	0.46	0.51



Society	Teta (reprod. primary kin)		Teta (total primary kin)	
	Females	Males	Females	Males
	(0.86-0.37)	(0.83-0.39)	(0.58-0.38)	(0.65-0.43)
Paiute	0.72 (0.92-0.58)	0.70 (0.87-0.56)	0.61 (0.7-0.54)	0.66 (0.74-0.59)
Apache	0.59 (0.7-0.54)	0.65 (0.79-0.6)	0.51 (0.55-0.47)	0.56 (0.6-0.53)
Takamiut	0.52 (0.78-0.36)	0.56 (0.85-0.39)	0.43 (0.52-0.37)	0.49 (0.6-0.41)
Hadza	0.57 (0.66-0.47)	0.66 (0.78-0.57)	0.51 (0.56-0.47)	0.58 (0.66-0.56)
Hill Pandaram	0.71 (0.85-0.59)	0.75 (0.87-0.64)	0.60 (0.67-0.55)	0.70 (0.77-0.64)
Miwuyt (Yolngu)	0.71 (0.9-0.56)	0.80 (0.97-0.62)	0.65 (0.75-0.56)	0.78 (0.92-0.67)

**Table S1:** Estimated MPCR thresholds, ‘Teta’, for reproductive primary kin (siblings and offspring) only and for total primary kin (siblings, offspring, and parents). In brackets: upper and lower estimates calculated by using the upper and lower bounds of the 95% confidence intervals reported by Hill et al., 2011, Science 331(6022): pp. 1286-1289. Where data were missing in the original data set these were assumed to be zero to receive the most conservative estimate.



**Figure S1:** Estimated threshold values for the minimum marginal per capita return required to make investing in the provision of linear public goods an optimal strategy in the presence of primary kin (parents, siblings and own offspring) for the 32 hunter-gatherer societies censused by Hill et al. 2011; separate lines for male and female target individuals; same order of societies as in Figure 1 of main article; error bars show upper and lower estimates based on the 95% confidence intervals reported by Hill et al..