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**ANCESTRAL KINSHIP PATTERNS SUBSTANTIALLY
REDUCE THE NEGATIVE EFFECT OF INCREASING
GROUP SIZE ON INCENTIVES FOR PUBLIC GOODS
PROVISION**

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Ancestral kinship patterns substantially reduce the negative effect of increasing group size on incentives for public goods provision

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Abstract: Phenomena like meat sharing in hunter-gatherers, self-sacrifice in intergroup conflicts, and voluntary contribution to public goods provision in laboratory experiments have led to the development of numerous theories on the evolution of altruistic in-group beneficial behavior in humans. Many of these theories abstract away from the effects of kinship on the incentives for public goods provision, though. Here, it is investigated 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 linear public goods game. Using recent anthropological data sets on relatedness in 61 contemporary hunter-gatherer and horticulturalist societies the relevant parameters of this model are then estimated. It turns out that the kinship patterns observed in these societies substantially reduce the negative effect of increasing group size on incentives for public goods provision. It is suggested, therefore, that renewed attention should be given to inclusive fitness theory in the context of public goods provision also in sizable groups, because its explanatory power with respect to this central problem in the evolution of human cooperativeness and altruism might have been substantially underrated.

JEL: B15, C72, D64, H41

Keywords: public goods; inclusive fitness; altruism; relatedness; kinship

Notes: All data on relatedness used in this paper are available in the online Supporting Information to Hill et al. 2011 (doi: 10.1126/science.1199071) and in the main article of Walker 2014 (doi: 10.1016/j.evolhumbehav.2014.05.003). I thank Max Albert, Matthias Greiff, and Eckart Voland for valuable discussions. All remaining errors are mine.

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1. Introduction

The high levels of cooperativeness and altruism observed in humans have been a prominent subject of research in social psychology, economics, evolutionary biology and anthropology in the last decades (Kurzban, Burton-Chellew, & West, 2015; Nowak, 2012; West, Griffin, & Gardner, 2007a). Phenomena like food sharing by hunter-gatherers (Hawkes, 1993; Hill, 2002), self-sacrifice in intergroup conflicts (Rusch, 2013a, Rusch, 2014), and voluntary contribution to the production of public goods in economic laboratory experiments (Chaudhuri, 2011; Fehr & Gächter, 2002) 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, & Vicente, 2014; Ohtsuki, 2014), usually because they followed a standard research heuristic which states that relatedness cannot explain cooperation and altruism in sizable groups. Instead, previous studies have focused, e.g., on direct and indirect reciprocity (Roberts, 2008), sanctioning institutions (Gürerk, Irlenbusch, & Rockenbach, 2006), assortment (Fletcher & Doebeli, 2009), or (cultural) group selection (Nowak, 2006).

The aim of this article is to develop one single argument in-depth. This argument is: The negative effect of increasing group size on the incentives for public goods provision under ancestral living conditions might have been overestimated in previous theoretical research on the evolution of human in-group beneficial behaviors, precisely because much of this research has abstracted away from kinship patterns.

To this end, this article clarifies the theoretical framework to be used and briefly reviews relevant recent research on public goods provision in Section 2; presents and analyses a simple mathematical model of the costs and benefits of public goods provision in groups which include kin in Section 3; and estimates this model's relevant parameters using recent anthropological data in Section 4. Section 5 discusses limitations and potential applications of the argument presented and highlights directions for future research.

If the argument developed here proves to be sound, it strongly reinforces one existing explanation for why we observe such high levels of individually costly behaviors to the benefit of in-groups in humans. It will be argued in the following that remarkably costly behaviors can have been positively selected for through kin-selection under realistic ancestral conditions. Thus, if our proximate motivational mechanisms and decision strategies for public goods provision still reflect these evolutionarily utmost relevant conditions, the frequently observed human readiness to benefit one's in-group at a cost to oneself is explainable as an adaptive behavioral trait which likely was under strong (kin-)selection during most of our species' (pre-)history.

2. Principles of inclusive fitness theory and previous research

2.1 Inclusive fitness theory

In the study of the evolution of behavioral traits in animals in general, it has proven fruitful to distinguish four basic categories of social behaviors by their respective direct fitness consequences for the acting individual (West, Griffin, & Gardner, 2007b): *mutually beneficial*, ‘+/+’, behaviors benefit both the acting individual, ‘actor’ for short, and all others affected by the actor’s behavior, ‘recipients’ for short; *s spiteful*, ‘−/−’, behaviors are costly to both actor and recipients; *selfish* behaviors, ‘+−’, benefit the actor at a cost to the recipients; and *altruistic* behaviors, ‘−/+’, finally, benefit the recipients at a cost to the actor. It is important to note that this terminology, which will be used throughout this article, uses *direct* fitness consequences to define the four basic categories. Conventionally, *direct fitness* is defined as the expected number of copies of own genes which an individual is able to transfer to the next generation through own reproduction (e.g., for humans having x children will yield $0.5 \cdot x$ expected copies of any given parental gene in the filial generation, as each child, in expectation, carries half of each of its parents’ genes).

As Hamilton (1964) pointed out, however, an individual’s *indirect fitness* also counts towards the eventual evolutionary fate of the genes this individual is carrying. Indirect fitness is defined as the additional expected number of copies of own genes which an individual transfers to the next generation by aiding the reproduction of relatives (Gardner & West, 2014). Thus, e.g., if a human can help one of its full siblings to sire one more child this yields an indirect fitness benefit of 0.5^2 for the helper, as, in expectation, the helper shares half of its full sibling’s genes and the sibling will pass half of them on to the child. Thus, in expectation, the additional niece or nephew carries 25% of the helper’s genes which then count into the helper’s indirect fitness balance. It is important to note, though, that indirect fitness only comprises the *additional* reproductive success of relatives which is caused by the actions of the helper; in other words, any child which a full sibling can have without the support of the helper does not count into the helper’s indirect fitness balance. The *inclusive fitness* of an individual, finally, is just the sum of its direct and its indirect fitness.

It is this conceptual framework of inclusive fitness, now, in which Hamilton’s famous rule for the evolution of altruistic behavior under kin-selection must be interpreted (Hamilton, 1964): If a gene coding for altruistic behavior causes a direct fitness cost, c , to its bearer, this gene can still spread in a population through kin-selection, as long as its indirect fitness benefit, $b \cdot r$, outweighs this direct cost, i.e. as long as $b \cdot r > c$, where b is the direct fitness benefit to a relative and r the relatedness coefficient of the altruist and the benefiting relative.

Hamilton’s insights into the workings of natural selection on groups of genetically related individuals have stimulated a plethora of studies on the inclusive fitness effects of social behaviors across species (Bourke, 2014) and under various ecological conditions (see, e.g., Taylor & Maciejewski, 2014). The application of inclusive fitness theory to the evolution of

human social behaviors has remained controversial, though, despite its remarkable explanatory power and the numerous successes it has already achieved (Rushton, 2009). In the following, nevertheless, this framework of inclusive fitness theory will be applied to one of the central problems which previous research on the evolution of human cooperativeness and altruism has tried to solve: the (voluntary) provision of public goods.

2.2 Previous research on public goods provision

Ever since Hardin's famous work on the tragedy of the commons (Hardin, 1968), at the latest, the problem of how human groups can manage to sustain communally shared resources, like forests and hunting or fishing grounds, has received much scientific attention (see, e.g., Ostrom, 1990). It is impossible to do justice to this extensive interdisciplinary library of research results in any brief format (see, e.g., Ostrom, 2014 for a recent introduction to this field). However, there is one very interesting point to note about this strand of literature: Many theoretical contributions on the question of how human groups can sustain cooperation in the face of strong individual incentives to free ride on collective efforts abstract away from the relatedness structure of these groups (see, e.g., Nowak, 2006 and Nowak, 2012 for overviews).

Of course, there are good reasons to do so. For one, contemporary industrial societies usually are characterized as large, functionally differentiated, and vastly anonymous, i.e. as not being based on cooperative kin networks. Nevertheless, societal institutions exist, and are upheld, which sustain and enforce cooperative collective norms, like tax payment, sanctity of contracts, the right to physical integrity, etc. Thus, one might argue that for understanding how and why these institutions endure, kinship cannot be too relevant. Furthermore, it can be shown mathematically, that with increasing group size, expected average relatedness in a group converges to zero (Lukas, Reynolds, Boesch, & Vigilant, 2005). Thus, in the study of public goods provision in sizable groups, its importance has been assumed to decrease rapidly with group size. Finally, including relatedness in models of collective action, in any species, is mathematically quite intricate. This is due to the fact that problem complexity increases by dimensions, as soon as a model tries to keep track of all (genetic) kinship ties in a given group, or even population, of animals (Nowak, 2012; Ohtsuki, 2014). Thus, it is a scientifically good heuristic to abstract away from kinship patterns in order to avoid these technical complications as long as there is no good reason to assume that relatedness should matter for a given problem (but see, e.g., Lehmann, Keller, West, & Roze, 2007 and West, El Mouden, & Gardner, 2011 for discussions of unfortunate misunderstandings this heuristic has caused).

All these lines of argument in support of studying models of non-related individuals are sound and have their respective merits. However, when we introduce the assumption that the psychological mechanisms which account for the manifold instances of in-group beneficial behaviors we observe in contemporary humans were formed during our species' evolutionary history (El Mouden et al., 2014; Laland & Brown, 2011), then kinship becomes relevant,

because humans did live in rather small groups comprising many kin during most of our species' history (in fact, for about 95% of this time span, Hill et al., 2011; also see Section 4).

In the rest of this article, it will be argued that the, perfectly reasonable, frequent negligence of ancestral kinship structures in previous theories on public goods provision might have led to a common underestimation of the positive effects which relatedness can have on the evolution of individual readiness to incur costs in order to bring about benefits for in-group members. After a simple model of public goods provision has been developed in Section 3, and its parameters estimated in Section 4, it will be discussed, in Section 5, how these results could help to explain a number of noticeable observations recurrently made in previous research on human public goods provisioning behavior.

3. Theory: Costs and benefits of the production of public goods in kin groups

The most prevalent theoretical tool for analyzing the costs and benefits of individual behavioral strategies in the context of public goods provision and their evolution is the linear n-player public goods game (see, e.g., Fletcher & Doebeli, 2009; Killingback, Bieri, & Flatt, 2006; Suzuki & Akiyama, 2005 for examples). This 'gold standard' game will be used in this article, although it probably is the most extreme simplification of a collective action problem. Important limitations entailed by this modeling approach will be discussed in Section 5. Note, however, that using this game also has crucial advantages. First, the game is simple and can therefore be analyzed and extended rather conveniently. Second, because the game is so prevalent in previous theoretical studies, the results obtained in the following can easily be used to adapt the findings made in previous work on non-related individuals to groups of kin. Third, in the realm of all n-person public goods games the linear one-shot game used here is a special case in which direct and indirect fitness costs and benefits can be calculated straightforwardly and separated completely (Ohtsuki, 2014), which is a technical requirement for the following analyses.

3.1 The k-PGG model

In the n-player one-shot linear public goods game, PGG, each player can contribute an amount of $c_i \geq 0$ to public goods production, and 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 $m > 1$, the (marginal) productivity of the public good, added up, and then equally redistributed among all n players. Taking the derivative of this expression with respect to c_i yields that $\pi_i(c_i)$ will increase in c_i whenever $b \equiv m / n > 1$, i.e., whenever the marginal per capita return ('MPCR' for short, symbol: b), on investment is greater than one. For $m = n$, every contribution c_i is an equilibrium strategy because in this special case players are indifferent between contribution and non-contribution. If $m < n$, finally, the optimal strategy in this game is not to invest at all, i.e., $c_i = 0$. Thus, if $m < n$, the game represents an n-person prisoner's dilemma, because then

the individually optimal, dominant strategy is non-contribution, while the socially optimal and Pareto-efficient strategy profile is full contribution by all players.

Now, let us interpret this game in terms of fitness, i.e., let π_i and c_i denote expected numbers of copies of a gene which will be transferred to the next generation and assume that players can be related (Ohtsuki, 2014; van Veelen, 2009). 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’:

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

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. Taking the derivative of 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} is greater than one. (Note that if we assume that only one relative of the target player is present in the group the expression reduces to Hamilton’s inequality; Hamilton, 1964.) We can use this expression to obtain a specific threshold, θ_i , for the MPCR of the k-PGG for a given individual i : Positive contributions, $c_i > 0$, in this game are beneficial, i.e., profitable in terms of inclusive fitness, for individual i whenever $b > (\sum_{j=1}^n r_{ij})^{-1} \equiv \theta_i$. Moreover, if $b > \theta_i$, the optimal strategy for individual i , in fact, is full contribution to this specific public good. For comparison: in the PGG without relatives $\theta_i \equiv 1$ for all individuals, implying $m > n$ as the condition for contributing to be individually beneficial.

There are at least two interesting aspects of the k-PGG that should be studied: (i) What might the distributions of θ_i have looked like under ancestral conditions? This will be estimated in Section 4.1. (ii) How do individual incentives for public goods provision differ between the PGG and the k-PGG? Ideally, of course, this question should be answered for that particular range of parameter values, i.e. group sizes and kinship patterns, which characterize the living conditions of ancestral human groups.

3.2 The relationship of theta and group size in the k-PGG model

Before this second question is tackled using empirical data in Section 4.2, though, let us clarify what it precisely means. The most important characteristic of the PGG, i.e. in groups of non-relatives, with respect to the relationship of group size and individual incentives for public goods provision is the following: As $b \equiv m / n$, it follows that the MPCR b of the PGG declines rapidly with group size, given that m is held constant. Figure 1 illustrates this for two public goods characterized by two different values of m . Note that, although $m = 15$ is quite a

high productivity, obviously, it makes full contribution to this public good a beneficial strategy only up to group sizes of $n < 15$.

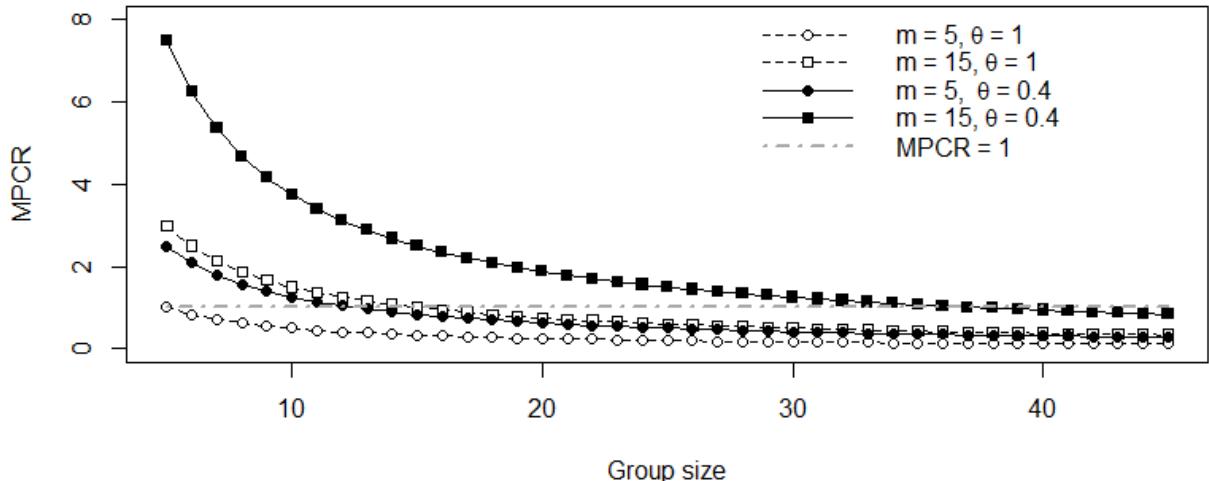


Fig. 1: Decline of the MPCR with group size in the PGG and the k-PGG

If, however, we look at the k-PGG, then the MPCR of a specific public good, characterized by its productivity m , is given as $m / (n \cdot \theta)$ and declines more slowly with group size. In Figure 1 this is illustrated for the assumption that θ is a constant with value 0.4, which corresponds, e.g., to an individual who is living in one group with two of its full siblings and two nephews or nieces. For the public good with $m = 15$, e.g., public goods provision then is individually beneficial for groups of sizes $n < 38$, which is more than twice the threshold value of the respective PGG. In addition, the assumption that θ is a constant is unrealistic, of course. More realistically, it should be assumed that θ is a decreasing function of the group size n (remember that $\theta_i = 1 / \sum_{j=1}^n r_{ij}$ and thus decreases with the number of relatives present in a group). In Section 4.2 such a function $\theta(n)$ will be estimated.

To summarize the theory part: The k-PGG model illustrates that when we analyze the costs and benefits of public goods provision under ancestral conditions, i.e., in groups which include a number of relatives, we need to take into account that an individual's contribution, c_i , to public goods provision repays not only directly, precisely: $\pi_i^D(c_i) = b \cdot c_i$, but also indirectly, precisely: $\pi_i^I(c_i) = b \sum_{j \neq i} r_{ij} \cdot c_i$. Analogously to Hamilton's rule, this implies that whenever $c_i < \pi_i^D + \pi_i^I$ holds, i.e. whenever the individual's direct fitness costs are offset by its inclusive fitness benefits, kin-selection can favor individually costly altruistic behaviors also when they benefit an individual's in-group as a whole. The aim of the following Section 4 is to estimate the levels of direct fitness costs up to which such altruistic in-group beneficial behaviors were likely to have been adaptive under ancestral conditions.

4. Evidence: Estimating the effect of kinship on the incentives for public goods provision under ancestral conditions

4.1 Estimating 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 directly estimate θ for average male and female target individuals in 32 contemporary foraging societies. Hill et al. provide 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.

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, in the following we will only use the average number of siblings, s , and the average number of offspring, o , to estimate θ , 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 θ , see Table S1 and Figure S1 in the supplemental materials. 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 θ s of 0.63 (± 0.11 SD) for female target individuals and of 0.60 (± 0.11 SD) for males. The individual estimates are displayed in Figure 2 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).

In all 32 societies surveyed the conservative θ -estimates are thus remarkably smaller than one, which is the benchmark MPCR value that should rule public goods provision strategies in one-shot PGGs with no kin present. On average, only roughly 60% of direct fitness invested need to be returned to the investor directly. The indirect benefits induced by kinship structure suffice to compensate him or her for the gross loss of the other 40%.

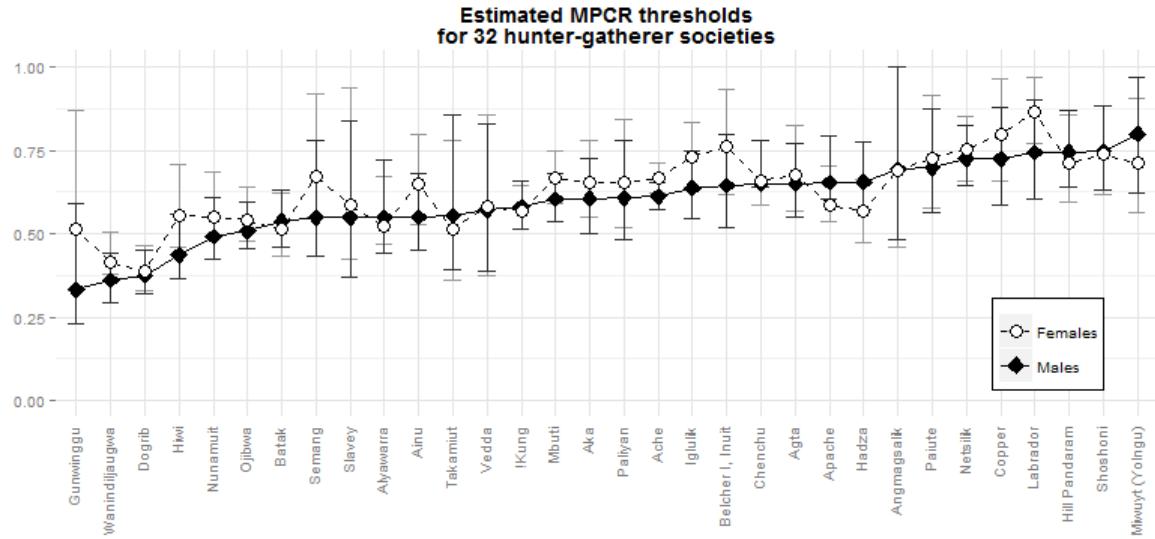


Fig. 2: Estimated threshold values, ‘thetas’, for the minimum marginal per capita return required to make contribution to the provisioning of linear public goods a beneficial strategy in the presence of reproductive primary kin (siblings and own offspring) for the 32 hunter-gatherer societies censused by Hill et al. 2011; separate lines for average male and female individuals; sorted increasingly, left to right, by thresholds for average males; error bars show upper and lower estimates based on the 95% confidence intervals reported by Hill et al..

4.2 The empirical relationship of theta and group size

While we have just seen that θ substantially lies below one in all of the societies survey by Hill et al., we do not yet know, how theta changes with group size. Fortunately, Hill et al. also report data on the average band sizes, n , they observed in the surveyed societies. When regressing θ on band size, a clear pattern can be observed: As suspected, θ shows a significant negative relationship with n ; regression results are shown in Table 2. (Because group sizes follow a skewed distribution in the data, see Fig. S2, a log-model is also included here to control for outlier effects.)

Using these estimates, we can now revisit the question raised in Section 3.1: How do the incentives for public goods provision change from the PGG to the k-PGG? As the estimated coefficients for males and females do not differ too drastically, this will only be done for ‘the average’ individual in the data collected by Hill et al. For this individual, theta roughly decreases with n as given by: $\theta(n) = 0.7 - (4/1000) \cdot n$. Figure 3 shows how this relationship of theta and group size affects the minimal productivity, m_{min} , required for a public good to represent a ‘profitable investment option’ in terms of inclusive fitness for an individual member of a group of size n (n ranges from 5 to 82 here, which is the interval of band sizes observed by Hill et al.).

IV: Av. Theta (reproductive kin only)		Males	Females
<i>Model 1</i>	<i>Intercept</i>	B = .689 (SE = .031) p < .001	B = .721 (SE = .029) p < .001
	<i>Band size</i>	B = -.004 (SE = .001) p = .001	B = -.004 (SE = .001) p = .001
<i>Model 2</i>	<i>Model fit</i>	adj. R ² = .268	adj. R ² = .302
	<i>Intercept</i>	B = .933 (SE = .090) p < .001	B = .935 (SE = .087) p < .001
	<i>log</i> ₁₀ (<i>Band size</i>)	B = -.255 (SE = .067) p = .001	B = -.231 (SE = .065) p = .001
	<i>Model fit</i>	adj. R ² = .299	adj. R ² = .274

Table 2: Results of linear regressions, independent variable: Theta (calculated using reproductive primary kin only), separately for males and females, N = 32 observations each; Model 1: $\theta = \text{intercept} + B \cdot (\text{'av. band size'})$; Model 2: $\theta = \text{intercept} + B \cdot \log_{10}(\text{'av. band size'})$

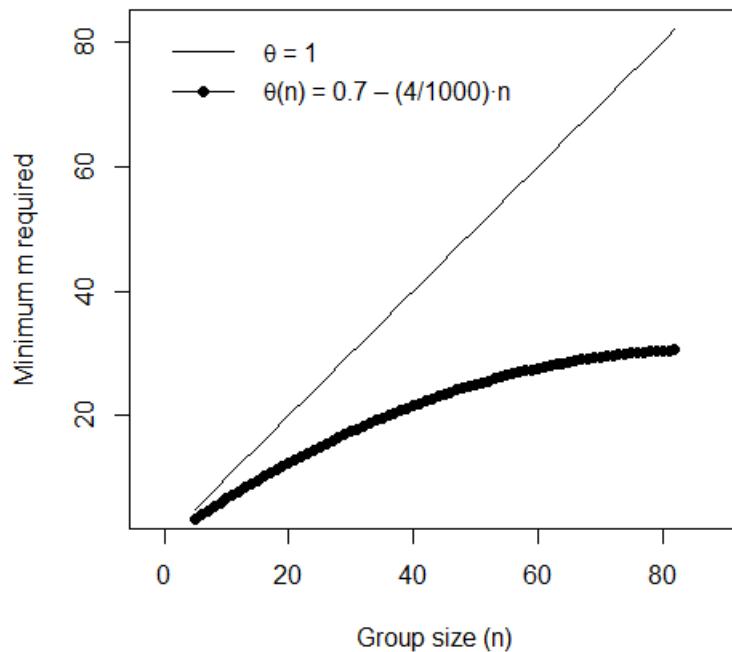


Fig. 3: Minimum productivities required for a public good to be profitable in terms of inclusive fitness as a function of group size. Straight line: if no kin are present, line with points: if estimated realistic numbers of kin are present (based on Hill et al.'s data)

As can be seen from Figure 3, particularly for larger groups, the m_{min} 's differ substantially between the PGG and the k-PGG. In the extreme case of $n = 82$, e.g., a productivity $m > 82$ would be required in the PGG for contribution to pay off individually, whereas in the

respective k-PGG m would only need to be larger than roughly 30.5, which is a little more than one third of the required productivity in the PGG.

4.3 Out of sample testing: A second estimate using complementary data

The data collected by Hill et al. already support the main argument of this article that the incentives for public goods provision under ancestral conditions might have been stronger than previously assumed. However, as with any data set, it could be argued that the observed patterns are due to a limitation of the sample. And in fact, the Hill et al. data only comprise the numbers of primary kin in contemporary hunter-gatherer societies. In order to cross-test whether the patterns just described generalize to a larger sample, the analyses will be repeated in the following using complementary data from a recent study by Walker (2014) which includes a number of additional hunter-gatherer societies not surveyed by Hill et al. and 24 additional horticulturalist societies (58 societies overall). Apart from the mean observed group size, this study, however, reports the estimated average coefficient of relatedness, r_a , for the groups in the sample. This is an advantage of this data set, because r_a not only includes primary kin but also more distantly related kin. Nevertheless, the availability of only this aggregate measure of relatedness forces us to use another method to estimate θ for this sample, namely: $\theta = 1 / [(n - 1) \cdot r_a + 1]$. That means, we simply assume that $r_{ij} = r_a$ for all $i \neq j$ (r_{ii} still is 1, of course).

Using this estimation method, we find that the average θ in the overall sample is 0.42 (± 0.17 SD) and thus lower than in the Hill et al. sample. This was to be expected, though, as we conservatively estimated upper bounds using the former data set. As Walker reports in his study, relatedness among horticulturalists in his sample is higher than among hunter-gatherers, and this is also reflected in a significant difference of the average thetas of these two subsamples ($t = 4.439$, $p < 0.001$); hunter-gatherers: av. $\theta = 0.49$ (± 0.14 SD), horticulturalists: av. $\theta = 0.31$ (± 0.16 SD). Regarding the relationship of theta and group size, we find the same patterns as in the Hill et al. data (overall sample: intercept = .533 (SE = .026), $p < .001$, group size B = $-.004$ (SE = .001), $p < .001$; see Table S2 for all regression results). Figure 4, finally, shows the empirical distribution of the minimal productivities required for public goods provision to be individually beneficial in all of the 61 societies for which data is available (i.e. combining the data from Hill et al. and the Walker data).

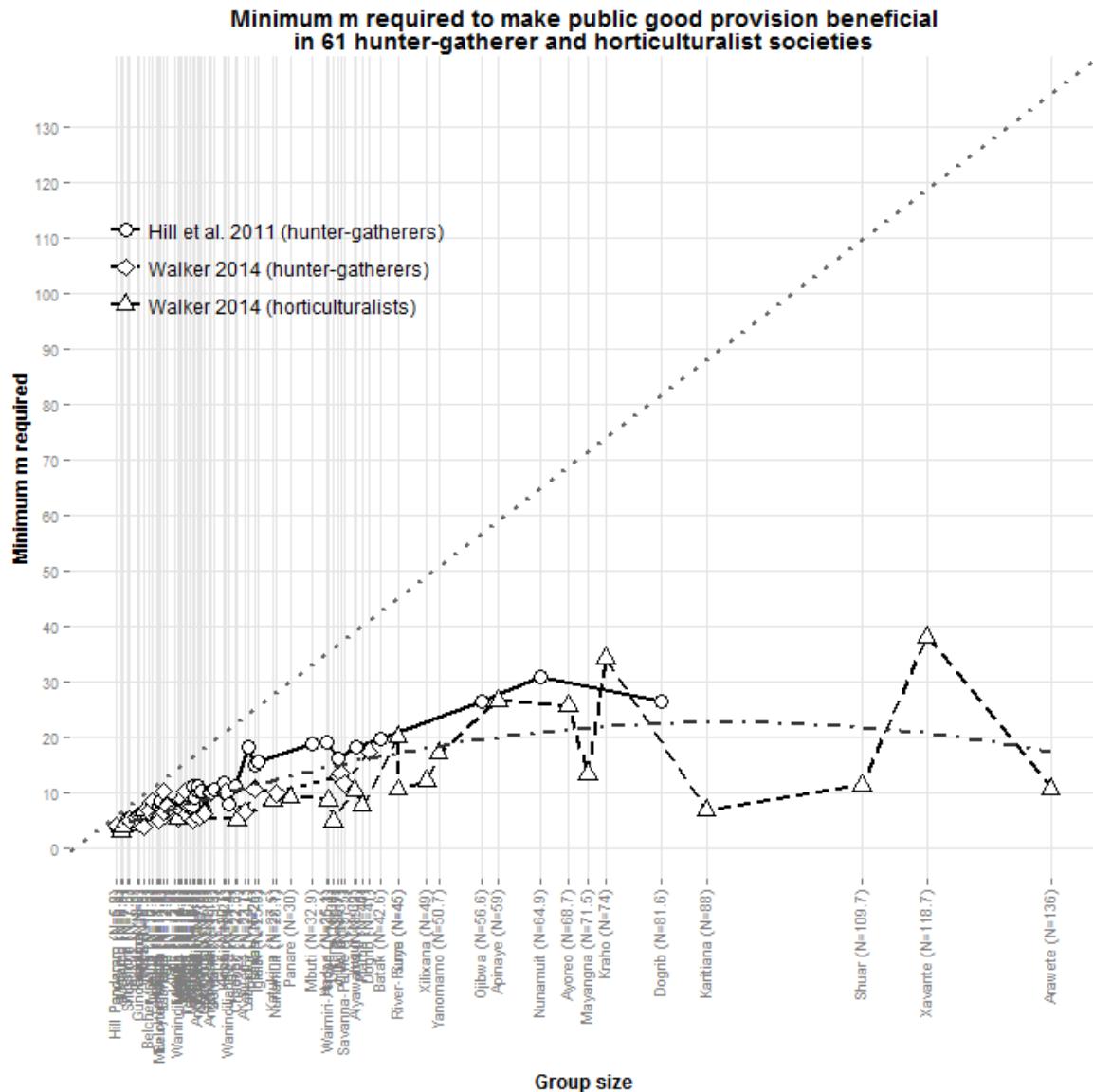


Fig. 4: Minimum productivities, m_{min} 's, required to make public goods provision individually beneficial over average group size in 61 hunter-gatherer and horticulturalist societies calculated based on data from Hill et al. (2011) and Walker (2014). Dash-dotted line: quadratic fit of $m_{min}(n)$ for the k-PGG for the complete sample; dotted line: $m_{min}(n)$ of the respective PGGs.

Figure 4 shows that increasing group size only slowly ‘crowds out’ incentives for public goods provision when relatedness is accounted for. In fact, when we linearly regress m_{min} on group size using all available data points (linear fit: $R^2 = 0.43$; not shown in Fig. 4), we find that it increases with a slope of roughly 0.18 which is a little less than one fifth of the slope it would increase with if inclusive fitness benefits were abstracted away from (dotted 45°-line in Fig. 4). Moreover, when we fit a quadratic function to the data (quadratic fit: $R^2 = 0.56$; dash-dotted line in Fig. 4), the data even suggest that this quadratic $m_{min}(n)$ of the k-PGG

might be decreasing again after having reached its maximum of about 23 at a group size of $n = 91$. As the observed variance increases and the data become much sparser for larger group sizes, though, this remains highly speculative.

5. Discussion

So far, it has been argued (i) that previous theoretical studies of the evolution of human public goods provisioning behavior have abstracted away from inclusive fitness effects of individually costly in-group beneficial behaviors under ancestral living conditions; (ii) and estimates of these effects have been presented which suggest that our ancestors might have faced much stronger incentives for public goods provisioning than one would suppose based on theoretical analyses not taking relatedness into account. In the remainder of this section, a number of previous empirical findings will be highlighted which could be interpreted as yielding additional support for the argument made here (Section 5.1), and the limitations of the model used will be critically discussed (Section 5.2).

5.1 Application: Explaining previous findings on public goods provisioning behavior

Although public goods games have been used in countless laboratory experiments now (see, e.g., Chaudhuri, 2011 for a recent review), only few of these studies directly investigate the two core components of the argument made here, i.e. relatedness and group size. This is because many of these studies investigate effects of additional factors like punishments and rewards (Frey & Rusch, 2012), self-selection (Gürerk et al., 2006), cross-cultural differences (Gächter, Hermann, & Thoni, 2010), etc. There is, however, a small number of studies which can be interpreted as tentative tests of the behavioral predictions yielded by the argument made here. These predictions are: (P1) Human subjects' intuitive strategies for public goods provision should not be as sensitive to changes in group size as one might suspect based on standard rational choice models (which do not take relatedness into account); instead, these strategies should be more sensitive to (P2) cues of relatedness and (P3) changes in the productivity of a public good when the group size is held constant.

With respect to (P3), the experimental economics literature unanimously reports that higher productivity of a public good results in higher voluntary contribution rates when group size is constant (see Ledyard, 1995 and Chaudhuri, 2011 for reviews). There is only a handful of studies, however, which have run public goods game experiments with large groups of subjects. Alas, all of these studies have held the MPCR constant, while manipulating group size. If at all, it is only very weak support for (P1), thus, that these studies find no significant decline of subjects' voluntary contribution rates with group size (see Nosenzo, Quercia, & Sefton, 2015). Isaac and colleagues (Isaac, Walker, & Williams, 1994) even found that groups with 40 and 100 subjects provided public goods more efficiently than groups of 4 and 10 subjects. Similar observations were recently made in a study which used much smaller MPCRs than Isaac et al. (who used MPCRs of 0.3 and 0.75): Weimann et al. compared subjects playing in groups of 60 or 100 using public goods with MPCRs as small as 0.02 and

0.04 and found “a strong MPCR effect, but almost no group-size effect” (Weimann, Brosig-Koch, Hennig-Schmidt, Keser, & Stahr, 2012).

Unfortunately, the literature is similarly sparse with respect to the effects of kinship cues on cooperation levels in laboratory experiments. However, supporting (P2), two seminal studies found that facial similarity, a subtle cue of relatedness, can enhance cooperation in the trust game (DeBruine, 2002) and, crucially, also in a four-person one-shot public goods game (Krupp, DeBruine, Jones, & Lalumière, 2012).

Thus, although the studies just mentioned were designed independent of the argument made in this article, there already is tentative experimental evidence which supports the idea that the high importance of relatedness and its damping effect on the negative impact of group size on incentives for public goods provisioning under ancestral conditions may have shaped the intuitive decision strategies human subjects apply in PGG experiments. More research in this direction is definitely needed though.

5.2 Model limitations

The argument developed in this article can be criticized in numerous ways. (i) As just mentioned, supporting empirical evidence is sparse, still. More experimental investigations of the effects of group size in large groups and perceived relatedness on public goods provisioning strategies are indispensable. (ii) It has also already been mentioned that the data available on kinship patterns under realistic ancestral conditions is sparse, particularly for average group sizes greater than about 50. This currently precludes better estimates of the relationship of θ and group size. (iii) While the two foregoing points of criticism can be countered with intensified empirical research, a crucial theoretical issue of the argument presented here must also be highlighted. Trenchantly put: It is an open question whether the simple PGG model used here has any empirical relevance. Although similarly simple PGG models are ubiquitous in the economic, psychological, and biological literature, the question of whether they capture sufficiently many relevant aspects of the collective action problems humans were exposed to in their (pre-)history is being lively and controversially discussed (see, e.g., Burton-Chellew & West, 2013; Kümmel, Burton-Chellew, Ross-Gillespie, & West, 2010; Rusch, 2013b, Rusch, 2014). A full discussion of the arguments against the suitability of the PGG as a model of evolutionarily relevant problems of collective action cannot be given here. This, however, is also not necessary, if we restate the main argument developed here more precisely: Previous theoretical work on the evolution of human in-group beneficial behaviors *which is based on PGG models* likely has underestimated the damping effect of relatedness on the negative impact of increasing group size.

Finally, not only the PGG but also the extended k-PGG developed here has crucial limitations, of course. Maybe most importantly, the k-PGG abstracts away from within-group fitness competition. One of the most important insights gained from inclusive fitness theory is that relatives only have partially aligned fitness interests (Trivers, 1974) and that indirect

fitness benefits can be ‘cancelled out’ by the effects of between-kin competition within groups (see, e.g., Taylor, Lillicrap, & Cownden, 2011). In order for the inclusive fitness benefits modeled by the k-PGG to have any evolutionary relevance, thus, additional assumptions need to be introduced, like, e.g., between-group competition (Rusch, 2014) or effective mechanisms of kin-discrimination (Hatchwell, 2010). Now that the k-PGG has been developed, however, and an attempt been made at estimating its relevant parameters, extending the k-PGG to become a more realistic model of evolutionarily relevant collective action problems, like, e.g., group defense in violent intergroup conflicts or group protection against natural hazards, is possible and promises a deepening of our understanding of human in-group beneficial behaviors.

6. Conclusion

Public goods provision in human groups might not pose as difficult a puzzle as previously thought. If our intuitive strategies for individually costly in-group beneficial, i.e. altruistic, behaviors were shaped during the evolutionary phase during which we lived in groups comprising a number of our kin, the indirect fitness benefits attainable through benefitting these groups may have offset the direct fitness costs of doing so to ‘quite some’ extent also in sizable groups. It is an important task for future research, though, to further clarify how much ‘quite some’ actually is. The first estimates presented here will hopefully be supplemented and amended by additional data gathering efforts, e.g. for societies with different subsistence regimes and/or larger average group sizes, and refined models which make more realistic assumptions about specific public goods and population structure.

The marginal productivity of relevant public goods, e.g., a crucial component of the model presented here, should be operationalized and measured thoroughly (see, e.g., Hawkes, 1993 for an early discussion of how this could be achieved). Another important point to address in future research will be domain-specificity. In this article we have only analyzed abstract linear public goods with differing marginal productivities in groups of variable size. Realistically, different groups have access to and benefit from different public goods depending on their ecological and social environment. Some of these public goods will have been relevant permanently over evolutionary time, e.g., group defense and protection, while others will have mattered only sporadically. Therefore, it seems likely that our evolved psychology for public goods provision reacts more reliably in the context of collective action problems which were persistently relevant.

To conclude: The estimates presented here will hopefully draw renewed attention to inclusive fitness theory in the context of public goods provision in humans. It may turn out that we have substantially underrated its explanatory power with respect to this central problem in the evolution of human cooperativeness and altruism.

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Supplemental Materials

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

Society	<i>Theta (reprod. primary kin)</i>		<i>Theta (total primary kin)</i>	
	Females	Males	Females	Males
<i>Dogrib</i>	0.39 (0.46-0.33)	0.38 (0.45-0.32)	0.33 (0.36-0.3)	0.32 (0.35-0.3)
<i>!Kung</i>	0.57 (0.64-0.51)	0.58 (0.66-0.51)	0.48 (0.52-0.46)	0.48 (0.51-0.45)
<i>Shoshoni</i>	0.74 (0.88-0.62)	0.75 (0.88-0.63)	0.71 (0.78-0.65)	0.72 (0.8-0.65)
<i>Batak</i>	0.51 (0.62-0.43)	0.54 (0.63-0.46)	0.45 (0.49-0.41)	0.47 (0.51-0.43)
<i>Alyawarra</i>	0.52 (0.67-0.47)	0.55 (0.72-0.44)	0.45 (0.5-0.41)	0.48 (0.53-0.43)
<i>Vedda</i>	0.58 (0.86-0.37)	0.57 (0.83-0.39)	0.46 (0.58-0.38)	0.51 (0.65-0.43)
<i>Paiute</i>	0.72 (0.92-0.58)	0.70 (0.87-0.56)	0.61 (0.7-0.54)	0.66 (0.74-0.59)
<i>Apache</i>	0.59 (0.7-0.54)	0.65 (0.79-0.6)	0.51 (0.55-0.47)	0.56 (0.6-0.53)
<i>Takamiut</i>	0.52 (0.78-0.36)	0.56 (0.85-0.39)	0.43 (0.52-0.37)	0.49 (0.6-0.41)
<i>Hadza</i>	0.57 (0.66-0.47)	0.66 (0.78-0.57)	0.51 (0.56-0.47)	0.58 (0.66-0.56)
<i>Hill Pandaram</i>	0.71 (0.85-0.59)	0.75 (0.87-0.64)	0.60 (0.67-0.55)	0.70 (0.77-0.64)
<i>Miwuyt (Yolngu)</i>	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, ‘Theta’, 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.

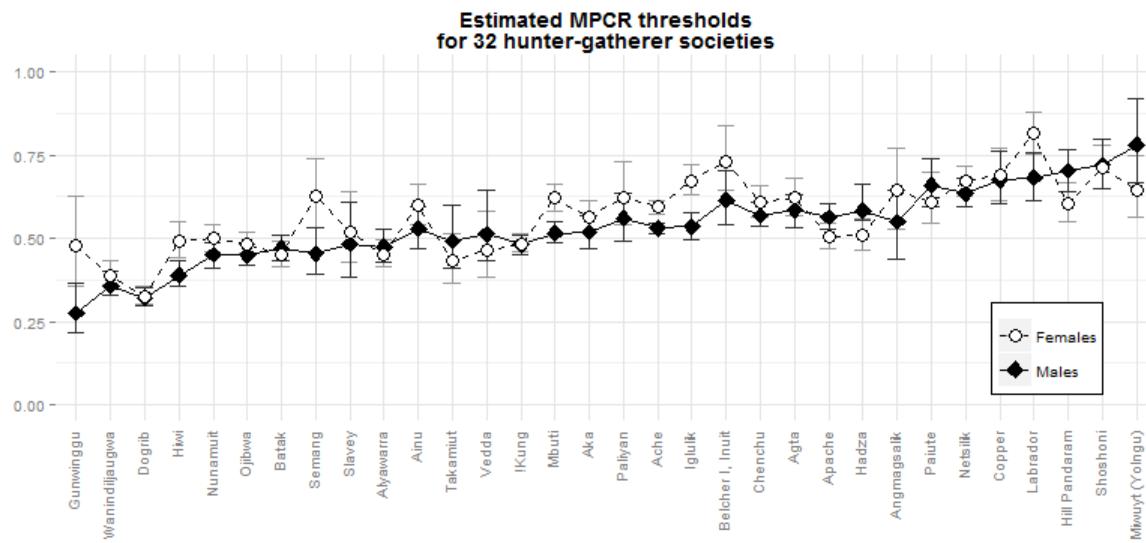


Figure S1: Estimated threshold values for the minimum marginal per capita return required to make investing in the provision of linear public goods an optimal strategy in the presence of primary kin (parents, siblings and own offspring) for the 32 hunter-gatherer societies censused by Hill et al. 2011; 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..

<i>IV: Av. Theta</i>	<i>Hunter-gatherers</i> (N=34)	<i>Horticulturalists</i> (N=24)	<i>Full sample</i> (N=58)
<i>Model 1 Intercept</i>	B = .655 (SE = .045) p < .001	B = .434 (SE = .047) p < .001	B = .534 (SE = .026) p < .001
<i>Band size</i>	B = -.009 (SE = .002) p < .001	B = - .002 (SE = .001) p = .005	B = - .004 (SE = .001) p < .001
<i>Model fit</i>	adj. R ² = .328	adj. R ² = .276	adj. R ² = .386
<i>Model 2 Intercept</i>	B = 1.031 (SE = .113) p < .001	B = .722 (SE = .107) p < .001	B = .909 (SE = .065) p < .001
<i>log₁₀(Band size)</i>	B = -.450 (SE = .093) p < .001	B = - .261 (SE = .067) p = .001	B = - .364 (SE = .046) p < .001
<i>Model fit</i>	adj. R ² = .425	adj. R ² = .385	adj. R ² = .516

Table S2: Results of linear regressions for the Walker 2014 data, independent variable: Theta; Model 1: $\theta = \text{intercept} + B \cdot (\text{'av. band size'})$; Model 2: $\theta = \text{intercept} + B \cdot \log_{10}(\text{'av. band size'})$

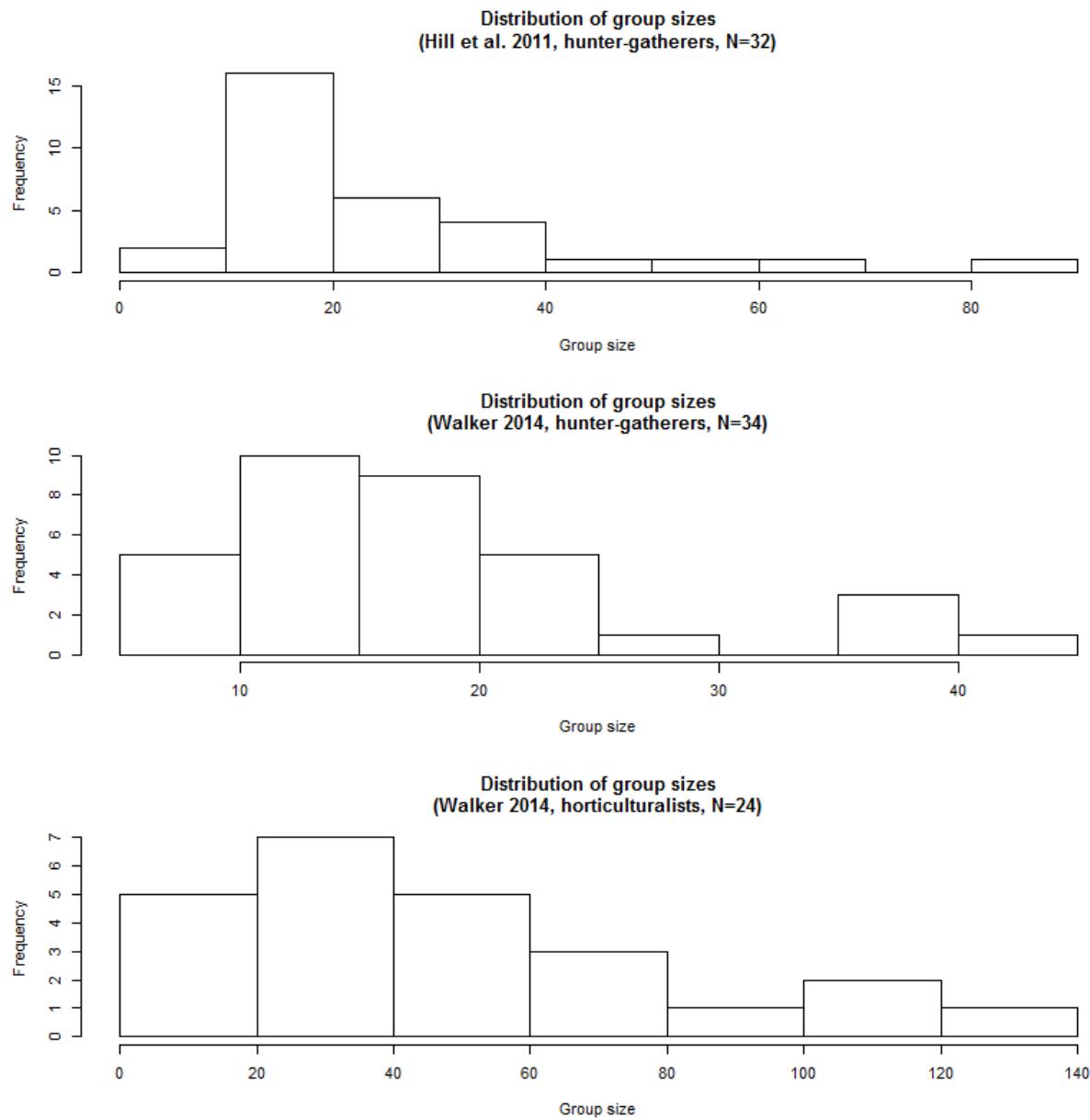


Figure S2: Distributions of the observed average group sizes in the data sets used.