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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

Numerous theories on the evolution of altruistic in-group beneficial behavior in humans exist. Many of these abstract away from the effects of kinship on incentives for public goods provision, though. Here, a simple model is devised that illustrates 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 contemporary hunter-gatherer and horticulturalist societies the parameters of the model are 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.

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## 1. Introduction

The high levels of cooperativeness and altruism observed in humans have been a prominent subject of research in economics, psychology, evolutionary biology, and anthropology in the last decades (Bowles & Gintis, 2011; Kurzban, Burton-Chellew, & West, 2015; Nowak, 2012; West, Griffin, & Gardner, 2007a). Phenomena like food sharing by hunter-gatherers (Hackman, Munira, Jasmin, & Hruschka, 2016; Hawkes, 1993; Hill, 2002), self-sacrifice in intergroup conflicts (Rusch, 2013a, 2014a,b), and voluntary contribution to the production of public goods in economic laboratory experiments (Chaudhuri, 2011; Fehr & Gächter, 2002; Zelmer, 2003) 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

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institutions (Güerke, Irlenbusch, & Rockenbach, 2006, 2014), 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 analyzes a simple mathematical model of the costs and benefits of public goods provision in groups that 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.

Although this paper focuses on ancestral living conditions, assuming that it is this 'environment of evolutionary adaptiveness' that shaped many elementary parts of our social behavioral repertoire and the motivational psychology controlling it (Kanazawa & Savage, 2009; Tooby & Cosmides, 2010; Tooby, Cosmides, & Price, 2006), kinship bonds obviously still are an important component of contemporary societies (Höllinger & Haller, 1990). While they may no longer have a noticeable role in sustaining society-wide cooperation in industrialized countries, they are essential to many economic activities at more local levels (Becker, 1991) and in developing countries (Bowles & Posel, 2005; Volland, 2011). According to recent estimates, e.g., roughly 90% of all farms world-wide are family farms, possibly still reflecting a shift in kinship patterns that occurred with the advent of horticultural subsistence (i.e. the earliest forms of farming; Walker, 2014) and may have played a key role in the emergence of agricultural economy (Rusch & Volland, 2016). In the developing world, furthermore, many small businesses operate through the work of family members that have no specified salary and extended family networks are important informal alternatives to institutionalized credit and labor markets (Banerjee & Duflo, 2007). Thus, also in large parts of today's world, biological relatedness has an important role in the mobilization of collective economic efforts, including voluntary communal public goods provision (see, e.g., Volland, 2011; Whyte, 1996).

## 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; *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 that an individual is able to transfer to the next generation through own reproduction, i.e. excluding reproduction caused by help from third parties (e.g., for humans having  $X$  children will yield  $0.5 \times X$  expected copies of any given parental gene in the filial generation, as each child, in expectation, carries half of each of its parents' genes; also see West et al., 2007a).

As Hamilton (1964) pointed out, however, an individual's *indirect fitness* also counts toward 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 that an individual transfers to the next generation by aiding the reproduction of relatives (Gardner & West, 2014). If, e.g., a human can help one of its full siblings to sire one more child this yields an indirect fitness benefit of  $0.5 \times 0.5 = 0.25$  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 that is caused by the actions of the helper; in other words, any child that 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 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,  $b \times r$ ,

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