



Original Article

Kin selection and ethnic group selection

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ABSTRACT

Ethnicity looks something like kinship on a larger scale. The same math can be used to measure genetic similarity within ethnic/racial groups and relatedness within families. For example, members of the same continental race are about as related ($r = 0.18\text{--}0.26$) as half-siblings ($r = 0.25$). However (contrary to some claims) the theory of kin selection does not apply straightforwardly to ethnicity, because inclusive fitness calculations based on Hamilton's rule break down when there are complicated social interactions within groups, and/or groups are large and long-lasting. A more promising approach is a theory of ethnic group selection, a special case of cultural group selection. An elementary model shows that the genetic assimilation of a socially enforced cultural regime can promote group solidarity and lead to the regulation of recruitment to groups, and to altruism between groups, based on genetic similarity – in short, to ethnic nepotism. Several lines of evidence, from historical population genetics and political psychology, are relevant here.

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1. Introduction

The theory of kin selection is a central pillar of the current evolutionary synthesis. The theory is important because it explains the widespread phenomenon of kin altruism – the evolution of behaviors geared to the survival and reproduction of an individual's kin, at the expense of the individual's own survival and reproduction.

Ethnicity and ethnocentrism in human societies share some affinities with kinship (Connor, 1993; Horowitz, 1985; Weber, 1978). Ethnic group members often maintain, rightly or wrongly, that they are descended from a common set of ancestors. They often use the idiom of kinship for one another – fellow ethnics are “brothers” and “sisters.” Ethnic identity, like kinship, is commonly seen as a primordial, ascribed, essential status, not easily changed. And ethnic group relations, like relations among kin, often seem to involve something more – and more primal – than the rational pursuit of individual or class interests.

All this has suggested to some evolution-minded authors that ethnicity is kinship, and that the evolution of ethnic sentiments can be explained by the theory of kin selection. An ethnic group is an extended family (so the argument goes), and ethnocentrism is kin altruism, advancing ethnic genetic interests through *ethnic nepotism* (Harpending, 2002; Rushton, 2005; Salter & Harpending, 2013; Shaw & Wong, 1989; Van Den Berghe, 1981; Vanhanen, 1999; Whitmeyer, 1997). It would be an important development in social theory if any of this turned out to be the case. Is this a real possibility? In the next three sections of this paper, I argue that the answer is *No*, *Yes*, and *Maybe*.

1.1. No

One argument for equating ethnicity and kinship is theoretical. The same mathematical machinery can be used to quantify genetic similarity within individuals and families, and within larger groups ranging from local subpopulations to continent-scale races. Insofar as ethnic groups correspond to population subdivisions, the population genetic definitions of kin relatedness and ethnic group relatedness are the same, allowing for a change of variables. This equivalence suggests that – following the theory of kin selection and assuming that ethnic group relatedness is high enough – we might predict significant altruism within ethnic groups. This possibility is taken up in the next section, where the verdict is negative. In spite of the formal correspondence, there is a quantitative difference between families and ethnic groups that prevents a straightforward application of the theory of kin selection to ethnicity.

1.2. Yes

The subsequent section arrives at a more positive assessment. It presents an alternative theory in which ethnic nepotism is socially enforced, and favored by ethnic group selection, a subtype of cultural group selection. According to the theory, members of an ethnic group may be cooperative and altruistic toward fellow ethnics based on shared genes. But shared genes are not just a result of genealogical connections, as they are in the standard theory of kin selection. Instead, a theory of ethnic nepotism must take into account some special evolutionary processes at work in human social evolution.

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1.3. Maybe

Ethnic group selection is a theoretical possibility; it might or might not have been of any importance in human evolution. Section 4 briefly reviews a few pertinent lines of evidence, from historical population genetics and political psychology.

2. From kin groups to ethnic groups

2.1. Relatedness and inbreeding

Hamilton's rule is a simple formula, central to the theory of kin selection (Hamilton, 1964). This section begins with the standard exposition of the rule, and how relatedness relates to inbreeding. The rest of the section shows that the rule can be tricky, so that applying it to ethnicity is not straightforward.

According to Hamilton's rule, an altruistic act that imposes cost c_j on benefactor j , while providing benefit b_i for beneficiary i , is favored by natural selection as long as

$$c_j/b_i < r_{ij} \cdot v_i/v_j \quad (1)$$

Here r_{ij} is the *coefficient of relatedness*: for a gene found in j , if k is the expected number of copies of the gene in j , then $r_{ij} \cdot k$ is the expected number of copies in i . If j is not inbred, then $k = 1$. If j is inbred, then $k > 1$. This counts only genes identical by descent over and above the genes i and j share as members of the same population. This version of Hamilton's rule also includes terms v_i and v_j , the *reproductive value* of recipient and donor, i.e. their expected genetic contribution to distant future generations. This might depend on their ages; we see in the next section why this matters.

The coefficient of relatedness is connected to another quantity, the coefficient of inbreeding, F (Falconer & McKay, 1996; Frank, 1998). The coefficient of inbreeding is, in the first instance, a measure of genetic similarity within a diploid individual, the probability that maternally and paternally inherited copies of a gene are identical by descent. We can write this as F_{jj} for individual j . The coefficient is greater than zero if j 's mother and father are related. For example if j 's parents are sister and brother, then $F_{jj} = 0.125$. Once again, this is over and above the probability that maternal and paternal copies are the same just because mother and father are members of the same population.

The coefficient of inbreeding can also be used to quantify genetic similarity within a subpopulation that is part of a larger population. This is usually written F_{ST} . If individuals tend to find mates in their own subpopulation, but to mate randomly *within* their subpopulation, then the probability F_{jj} that maternal and paternal copies of a gene in individual j are identical by descent is equal to the probability $F_{ij} = F_{ST}$ that two genes in randomly selected individuals i and j in the subpopulation are identical by descent.

The coefficient of relatedness and the coefficient of inbreeding are related by the formula

$$r_{ij} = 2 \cdot F_{ij} / (1 + F_{ij}) \quad (2)$$

where the $2 \cdot F_{ij}$ term takes into account that i , being diploid, has two chances of having genes identical by descent with a gene in j , and the $1 + F_{ij}$ term takes into account that at homologous loci j may be identical by descent with herself through inbreeding.

Various authors have been interested in how coefficients of inbreeding and relatedness might relate to the evolution of human social behavior in groups larger than families. Some of their results are shown in Table 1, which gives summary statistics for F_{ST} 's for assorted human population subdivisions, as well as the corresponding coefficients of relatedness (column headed r_H) following Condition (2) with $F_{ij} = F_{jj} = F_{ST}$.

It is tempting to plug the r_H values in the table into Hamilton's rule, and predict kin altruism accordingly. Several of the authors cited in the table have done just this, reaching different conclusions depending on what level of population subdivision they think is evolutionarily important (Bell, Richerson, & McElreath, 2009; Harpending, 2002; Salter & Harpending, 2013).

We'll see below that things are not so simple.

2.2. Kin selection: socially enforced altruism

The simplest formulation of the theory of kin selection treats it as a one-player game, where an actor has the power to help one or more passive recipients. In this case (given some further assumptions; see below) the r 's derived from genealogies or from across the whole genome may predict behavior toward kin.

But the theory gets more complicated when there are strategic interactions between players. For example, imagine a game, in the game theory sense, played by two siblings. If the only thing one player knows about the other is that he is her brother, then she can expect that half his genes are identical by descent with hers. But if she also knows what strategy her brother has chosen, then this may raise or lower the estimated number of shared genes at loci affecting the choice of strategy (but not at other unlinked loci). It will be adaptive for her to raise or lower her level of altruism accordingly. In a case like this, neither genealogy nor genome-wide genetic similarity suffices to predict similarity at loci governing strategic behavior, and it is these loci that kin selection cares about. So one way the theory of kin selection gets tricky is when it's combined with game theory. Just assuming that game players keep score according to Hamilton's rule, with r 's based on genealogy, generally gives the wrong answer.

To some extent, each case that combines kin selection and game theory has to be analyzed separately. But there is a family of cases that can be treated more systematically – if sometimes approximately – involving *socially enforced nepotism* (Jones, 2000, 2016). Socially enforced nepotism happens when a group of individuals acts together to help another related group, without much or any expected return benefit.

Table 1
Inbreeding and relatedness: summary statistics.

Study	Type of society or population subdivision	Number of populations	Subdivision size Median (range)	F_{ST} Median (range)	r_H Median (range)	r_C Median (range)
Jones (2000)	Tribal populations	10	1875 (500–122,022)	0.030 (0.003–0.063)	0.058 (0.006–0.119)	0.822 (0.231–0.991)
Bowles (2006)	Foragers	13	–	0.076 (0.007–0.170)	0.141 (0.014–0.29)	–
Bell et al. (2009)	Adjacent nations	59 pairs	>10 ⁵	0.0032 (0.032–0.00044)	0.0064 (0.063–0.00088)	1.00
Salter and Harpending (2013)	Races	1 (<i>Homo sapiens</i>)	>10 ⁸	0.12 (0.10–0.15)	0.22 (0.18–0.26)	1.00

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