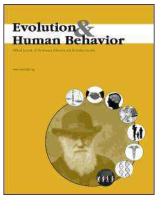
Evolution and Human Behavior xxx (2017) xxx–xxx

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org



Kin selection and ethnic group selection

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ARTICLE INFO

Article history:
Initial receipt 7 December 2016
Received in revised form 7 August 2017
Final revision received 23 August 2017
Available online xxxx

Keywords:
Kin selection
Ethnicity
Ethnocentrism
Cultural group selection

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 ($r = 0.18$–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.

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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https://doi.org/10.1016/j.evolhumbehav.2017.08.004

Please cite this article as: Jones, D., Kin selection and ethnic group selection, *Evolution and Human Behavior* (2017), https://doi.org/10.1016/j.evolhumbehav.2017.08.004

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

$$c_j/b_i < r_{ij} \cdot v_i/v_j \tag{1}$$

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

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

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 $1 + F_{jj}$ 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_G 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 (*Homo sapiens*)	$>10^8$	0.12 (0.10–0.15)	0.22 (0.18–0.26)	1.00

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(This is phrased as one group helping another group, but socially enforced nepotism can also involve a well-off segment of a kin group collectively enforcing a rule of helping needy group members who cannot reciprocate.) Socially enforced nepotism is distinct both from individual nepotism, where individuals act on their own to help kin, and from simple cooperation, where members of a group act together to their mutual advantage.

The idea behind socially enforced nepotism is that altruism toward kin is a public good. When someone pays a cost to provide a benefit for one of her kin, she is also providing a free inclusive fitness boost to the rest of the recipient's kin. If individuals act together to help their mutual kin, then natural selection favors a higher level of altruism, measured as a cost/benefit ratio, than if they act separately. Standard inclusive fitness calculations aren't guaranteed to give the right answers here (see, for example, the discussion of the Brothers Karamazov Game in Jones, 2016).

Socially enforced nepotism, like other public goods provisioning, requires enforcement. Several enforcement mechanisms have been proposed. Bowles (2006) argues that *reproductive leveling* in foraging societies amplifies kin altruism. Jones (2016) argues that reputation can operate as a kind of social currency, allowing kin groups to enforce an ethic of *generalized reciprocity*, in which needy kin get help even though they can give back little in return.

One way to get a handle on socially enforced nepotism is to recognize a group coefficient of relatedness, r_G, in addition to the more familiar individual coefficient of relatedness, r_H. The group coefficient of relatedness determines the expected level of altruism of members of a group according to the formula $c/b < r_G$, provided the members of a group act together. More precisely, r_H gives the exact break-even altruism ratio, c/b, provided that each group member has one vote regarding the amount of altruism carried out by the group, and the amount increases linearly with the number of *Yes* votes. But the formula is still approximately correct even with different voting rules and enforcement mechanisms (Jones, 2000).

Table 2 compares F, r_H, and r_G. Each of these variables is a coefficient of relatedness at some level, whether between genes (F), between diploid individuals (r_H), or between groups (r_G). And each variable is a regression coefficient. The expected number of genes identical by descent in a target unit – gene, individual, or group – equals the number of such genes in a focal unit, times the appropriate coefficient.

The right-most column of Table 2 shows how adjacent levels of relatedness are connected. Each equation there supplies a kind of "voter's guide." The first equation tells a gene how much individual altruism to "vote" for when it finds itself inside a diploid organism. The second equation tells an individual how much socially enforced nepotism to vote for when she finds herself inside a collectively acting group.

We'll see below that socially enforced altruism is also relevant to ethnicity. But first we take a detour.

2.3. Kin selection: the weak selection assumption

Strategic interaction is not the only factor that can throw off Hamilton's rule. Even if we ignore strategic interaction and consider only individual r_H's, we arrive at some odd conclusions if we're not careful.

Consider, for example, F and r_H for major continent-scale races (the last row in Table 1). The F values demonstrate a widely publicized result: members of different races are more alike than different (Lewontin, 1972). There is far more genetic variation within races than among them (90–85% versus 10–15% of total variance). The same figures, converted into r_H's, also demonstrate a less familiar result: members of the same race, relative to the species as a whole, are related to one another ($r_H = 0.18$–0.26) almost as closely as half-siblings ($r_H = 0.25$).

If we were to plug an r_H in this range into Hamilton's rule, we would predict high levels of altruism within major population blocs. Is this remotely plausible? Are random strangers of the same race in a multiracial society nearly as spontaneously altruistic to one another as a pair of half siblings, a grandparent and grandchild, or an uncle and niece in a racially homogenous society? Surely something has gone wrong here; standard kin selection theory is being misapplied somehow. It's not enough to claim that multiracial societies are an evolutionary novelty, so that human beings haven't had enough time to evolve the necessary adaptations. The fallacy runs deeper; even if humans had evolved in a multiracial setting, standard kin selection would not favor this sort of altruism. It's not that ethnic groups and races are categorically distinct from families. The same variables – coefficients of inbreeding and relatedness – can be used to quantify genetic variation both for small ephemeral groups and for large enduring ones. But there is a crucial quantitative difference between small and large groups. With increasing scale and time depth come increasingly serious violations of one of the assumptions made in deriving Hamilton's rule, the *weak selection assumption*.

According to the weak selection assumption, selection doesn't change the frequency of an altruism gene between the time it is present in any shared ancestors and the time it expresses itself in a descendant's altruistic act. We can see why this matters by dropping the assumption. Suppose, for example, that a woman has a chance to save the life of her full brother. Under the standard argument invoking Hamilton's rule, there is a probability of 0.5 that an altruism gene found in the rescuer is found in her brother as a result of their shared parentage, so she should save him, even at some risk to her own life, as long as his expected fitness gain, times 0.5, is greater than her expected loss. But now suppose that some of the potential rescuer's siblings have already died while altruistically rescuing some of her other siblings. Their deaths will have removed copies of the altruism gene from the family. The expected frequency of the allele among the survivors, including her imperiled brother, is now <0.5.

More realistically, selection doesn't usually change gene frequencies a lot in such a short period. For groups lasting several generations, up to the scale of small local kin groups, the weak selection assumption is likely roughly correct (Bowles, 2006). But over longer time scales, the assumption becomes increasingly unrealistic. Even slight fitness differences can accumulate to cause large changes in gene frequencies in long-lived groups. This is crucial with respect to the larger population subdivisions (nations and races) in Table 1, because the F values given in the table omit one key detail. These F's are valid for most genetic loci, which are not under strong selection. But for genes under selection, F's can be much lower or higher. For example, for genes governing pigmentation, directional selection has pushed populations much farther apart

Table 2
Inbreeding and relatedness: definitions and formulas.

Variable symbol	Variable name	Measures relatedness of …	Formula
F	Coefficient of inbreeding	One gene to another, within an individual, between kin,or within a subpopulation.	
r_H	Individual coefficient of relatedness	One diploid individual, i, to another, j.	$r_H = \frac{2F_{ij}}{1+F_{ii}}$
r_G	Group coefficient of relatedness	One group, i, to another, j, where r_H within $j = r_{jj}$ r_H between i and $j = r_{ij}$ and n's are group sizes	$r_G = \frac{n_i \cdot r_{ij}}{1+(n_j-1)r_{ii}}$

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than drift alone would have carried them (Sturm, 2009). This means that in really long-lived groups, the theory of kin selection only applies if selection is very weak. Very weak selection takes a very long time – many cycles of group formation and replacement – to change gene frequencies appreciably. And the end result – tiny altruistic benefits, tinier costs – is trifling.

This criticism, I think, is fatal to Salter and Harpending's (2013) case for ethnic nepotism. And the criticism applies in reverse to Bell et al. (2009). These authors argue that where the evolution of large-scale prosociality is concerned, we should be looking at *r*'s between adjacent nations, rather than among continent-scale races, as in Salter and Harpending. Because these *r*'s are low (they write), we can't expect much kin-based altruism at the level of ethnic groups or nations. But I argue instead that this is beside the point. Suppose the *r*'s between nations had been higher: this, on its own, would not license a prediction about kin altruism among ethnic groups. On a large scale, for non-trivial benefits and costs, neither set of *r*'s can be plugged into Hamilton's rule.

Other authors have criticized the argument that kin selection theory predicts ethnocentrism (Brigant, 2001; Dawkins, 1979). Here I have tried to explain both why the argument has appealed to some theoretically adept scholars and why it fails.

3. From cultural group selection to ethnic group selection

The standard theory of kin selection does not yield a theory of ethnic nepotism. In large, long-lasting groups, members may or may not have high coefficients of inbreeding and relatedness as a result of sharing multiple links to distant ancestors, but neither genealogical relatedness nor genetic similarity over the whole genome is a reliable guide to similarities at loci governing sociality. However, the fundamental insight behind the theory of kin selection – that natural selection can favor social interaction, including altruism, based on shared genes – could still be relevant even on the scale of ethnic groups, where shared genes may have more to do with the selection pressures associated with shared culture. This section develops a model to illustrate this.

The model here builds on previous work on cultural transmission and social evolution, and on the extensive literature (Richerson et al., 2016) making a theoretical and empirical case for cultural group selection. The model takes this work in a new direction, concentrating on what distinguishes ethnicity from large-scale cooperation in general, and on the parallels between ethnicity and kinship. It can be regarded as a follow up to my previous work on kinship norms and evolution. In that work I suggested – following a long-standing tradition in social anthropology – that what distinguishes kinship norms from other social norms is an ethic of unbalanced *generalized reciprocity* among kin, and I developed a model of kin altruism amplified by socially enforcement that might account for this. The present work is also about socially enforced altruism, but on a larger scale, where the weak selection assumption no longer holds. In contrast with much previous work, the focus is less on the sociological details of how norms are enforced, and more on the consequences of enforcement for evolution within and between groups. The result is a simple model that makes explicit some parallels between ethnic group selection and kin selection which are largely unexamined in earlier work. For example, we see that ethnic genetic relatedness, ethnic nepotism, and ethnic genetic interests can all be meaningful concepts.

We begin with a gene-free model of cultural group selection (Subsection 3.1). This is elaborated to distinguish ethnic group selection as a specific subtype of cultural group selection, resulting from the genetic assimilation of culture (Subsection 3.2). The remaining subsections highlight some contrasts between cultural group selection in general, and ethnic group selection. With cultural group selection, groups may expand either through natural increase or through recruiting outsiders. With ethnic group selection, genes make a difference, and recruitment (e.g. through exogamy) may be favored or disfavored depending on the genetic makeup of potential recruits, and the strength of selection producing genetic similarity within groups, potentially leading to policing of genetic boundaries between groups (Subsection 3.3).

Also, while most models of cultural group selection are meant to account for *cooperation*, with members of a group paying a cost to secure a collective good for all, the present model also covers collective *altruism*, with members of one segment of an ethnic group paying a cost to secure benefits for another segment (Subsection 3.4). This is socially enforced altruism. It depends on shared genes, and we define an ethnic coefficient of relatedness, r_E, between different segments of an ethnic group, comparable to the r's discussed above, but depending in this case on a segment's history of selection. This coefficient is determined by the ratio of altruism genes in donor and recipient. And it determines the ratio of donor costs to recipient benefits where altruism is concerned, although in a slightly complicated fashion, since the coefficient evolves over time.

The theory of ethnic group selection developed here does not cover everything falling under the heading of ethnicity. Some evolutionary models of ethnicity are concerned with trust and cooperation in dyads without ethnic group selection (Hartshorn, Kaznatcheev, & Schultz, 2013; McElreath, Boyd, & Richerson, 2003). Nor is the theory a general theory of social evolution. For example, much of the evolution of major missionary religions involves cultural group selection without ethnic group selection (Norenzayan, 2015). But the theory may provide insight into a range of phenomena, noted by scholars of ethnicity and ethnonationalism, that look something like kin altruism: human beings often identify with ethnic groups, that, in contrast to other social groupings, are defined by putative common descent. And people often organize to support the supposed interests of those groups, police group boundaries, and enforce altruism toward group members. The theory may also tie together some findings regarding the psychology of ethnocentrism, including individual-level variation (see especially Subsection 4.2).

3.1. The selection/defection balance

We begin with an elementary gene-free model of cultural group selection for provision of public goods. Consider a population of groups. A group may be in one of two cultural regimes, high or low solidarity, labeled U and V. In the high solidarity regime, U, each group member pays a cost *c* to make a contribution to a public good which results in benefit *b* for each. In the low solidarity regime V, group members neither pay the cost nor gain the benefit. Costs and benefits are measured in the currency of fitness, and $b > c$, so in regime U group members have fitnesses proportional to $1 + s_u$ with $s_u = b - c$. In regime V, group members have fitnesses proportional to 1.

With genetic evolution, natural selection in favor of an allele may be balanced by mutation pressure in the opposite direction. A similar balance may hold with cultural evolution. Suppose groups sometimes spontaneously transition from one cultural regime to the other. In each generation, a U group switches to V with probability *f*, and a V group switches to U with probability *h*.

For given values of s_u, *f*, and *h*, the equilibrium frequency, $\hat{u}$, of U is a solution to a quadratic equation. But here we use an approximation. We are most interested in the balance between cultural selection in favor of high solidarity (given by s_u), and cultural defection away from it (given by *f*). We assume that solidarity is prone to spontaneous decay, so s_u and *f* are the important variables. The opposite transition, from low to high solidarity (given by *h*), is infrequent. With *h* close to 0, $\hat{u}$ is approximately given by:

$$\hat{u} \approx 1 - f/s_u \quad \text{if} \quad f \leq s_u \tag{3}$$

$$\hat{u} \approx 0 \quad \text{if} \quad f > s_u \tag{4}$$

This is similar to the standard formula for mutation-selection balance in genetic evolution.

We can refine the model by considering evolution with more than one solidary regime. Suppose that in addition to the non-solidary regime V, there are two possible solidary regimes, U_1 and U_2, with associated frequencies u_1 and u_2 (where $u_1 + u_2 + v = 1$), selection coefficients s_{u1} and s_{u2}, and defection rates f_1 and f_2. Suppose $f_1/s_{u1} > f_2/s_{u2}$. Then the growth rate for U_1 is positive only up to $u_1 + u_2 < 1 - f_1/s_{u1}$, while the growth rate for U_2 is positive all the way to $u_1 + u_2 < 1 - f_2/s_{u2}$, so there is an interval where the rate is negative for U_1 and positive for U_2. In consequence, U_2, the solidary regime with a lower f/s_U, competitively excludes U_1. So as long as h is close to 0, cultural group selection favors the regime with the smallest f/s_U, in other words, with a combination of high fecundity (high s_U) and high transmission fidelity (low f).

3.2. Genetic assimilation

In the standard theory of kin selection, gene frequencies differ between groups as a result of sampling error. By chance, some families have more altruism alleles, others fewer. But in long lasting groups, within-group selection can be a more important influence on gene frequencies. Within-group selection can either undermine or strengthen selection on culture among groups.

Let us return to our population of groups under two cultural regimes, U and V. Now suppose that there are also two alleles, P and Q at one genetic locus. Suppose that in groups under regime U, the frequencies of P and Q are p and $q = 1 - p$. And suppose that P is favored by selection within U groups, so the fitness of P within the group is proportional to $1 + s_{p.}$, with $s_{p.} > 0$, while the fitness of Q is proportional to 1. As before, we are mostly interested in regime U. For regime V, we assume merely that transitions from V to U are rare ($h \approx 0$), and that selection within V groups keeps their frequency of P uniformly low.

Now suppose that in U groups, P is not only favored by selection, but also changes the fidelity of cultural transmission. In an all-Q group, the rate of defection from U to V is f, as before. But in an all-P group the rate is g. The relationship is linear, so in mixed groups the rate of defection is $g \cdot p + f \cdot q$.

Under these assumptions, P goes close to fixation in groups under regime U, and the new approximate equilibrium frequency of regime U is:

$$\hat{u} \approx 1 - g/s_u \quad \text{if} \quad g \leq s_u \tag{5}$$

$$\hat{u} \approx 0 \quad \text{if} \quad g > s_u \tag{6}$$

With regard to the effect of within-group selection on the evolution of solidarity, there are two cases to consider:

$$f - g < 0 \qquad \text{Discordant} \tag{7}$$

$$f - g > 0 \qquad \text{Concordant} \tag{8}$$

First take the discordant case. Suppose that in mixed groups, P manages to shift some of the cost of producing public goods onto Q. The benefit, b, of belonging to the group is still the same, as is the *average* cost, c, but for a carrier of allele P the cost is just $c - q \cdot s_{p.}$, while for a carrier of Q, the cost is $c + p \cdot s_{p.}$ where $0 < s_{p.} < c$. At the same time, with $g > f$, groups with higher p are more likely to give up on group solidarity altogether. So selection within groups in favor of P, the reluctant cooperator, also results in an increased rate of defection and a lower equilibrium u. Within-group selection could even result in high group solidarity largely disappearing. If $g > s_{p.} > f$, then the occasional groups that switch from V to U, beginning with a low frequency of P, will flourish for a while under cultural group selection, but will be overwhelmed by defection as group p's increase.

So far, we seem to have taken a roundabout route to discover that genetic altruism can't persist in groups much larger than families. This conclusion holds in large, long-lasting groups even with high values of F and r_H for selectively neutral genes, because selection erases between-group differences for altruism genes. Even a group that starts out by chance with an especially low frequency of the uncooperative P allele still winds up with a high frequency of P after generations of selection.

But now take the concordant case. If straight altruism can't evolve by group selection, socially enforced cooperation is another matter. Suppose we return to a population of groups under two cultural regimes, U and V, with two alleles, P and Q. We add social enforcement: the cost of solidarity, c, is the sum of two components: the cost, c_1, of contributing to public goods, and the cost, c_2, of enforcing a contribution. Total costs are still less than benefits, $s_U > 0$, where $s_U = b - c$. But this time we make P *more* committed to group solidarity, and assume that in mixed groups, regime U rewards the zealous P′s with a smaller share of the enforcement cost, $c_2 - q \cdot s_{p.}$, and punishes the half-hearted Q's with a larger share, $c_2 - p \cdot s_{p.}$, where $0 < s_{p.} < c_2$. At the same time, $g < f$, so groups with higher p are also less likely to give up on cooperation. Selection within groups in favor of P, the committed cooperator, also results in a lower rate of defection and a higher equilibrium u.

When genic natural selection for social enforcement is added to cultural group selection for solidarity, group solidarity can turn from rare to commonplace. If $f > s_u > g$, and h is close to 0, then groups will occasionally switch from low to high solidarity. With $f > s$, defection initially outweighs cultural group selection, and most of these groups defect from the high solidarity regime. But occasionally, by chance, a group persists in regime U for some time. In this case, P increases in frequency, asymptotically approaching $p = 1$. High frequencies of P stabilize solidarity in these groups, and they increase their share of the population, up to the point that cultural group selection, s_u, is balanced by the lower rate of defection, g.

We have described two different scenarios, in which natural selection within groups either undermines or reinforces cultural group selection. If enforcement costs are not too great, then groups that maintain the latter condition will prevail. Suppose two solidary regimes U_1 and U_2 have associated selection coefficients $s_1 = b - c_1$ and $s_2 = b - c_1 - c_2$, where c_2 is the enforcement cost. Regime U_1, which entails lower costs and a higher between-group selection coefficient, has the advantage initially. But U_2 wins ultimately if selection within groups leads to a sufficiently low defection rate for U_2 relative to U_1, i.e. if $g_1/s_1 > g_2/s_2$, in spite of $s_1 > s_2$, where g_1 and g_2 are the respective defection rates after within-group selection.

What we have outlined here is a group-level version of a familiar evolutionary phenomenon, genetic assimilation (Crispo, 2007; Ehrenreich & Pfennig, 2015). In the standard individual-level version, an organism produces a novel adaptive behavior as a result of learning or other developmental plasticity. Over time, natural selection favors genes that make it easier to acquire the behavior, so the adaptive behavior is produced consistently rather than sporadically. Eventually a learned adaptation becomes instinctive, not through Lamarckian evolution, but through natural selection. Cultural transmission is a special form of developmental plasticity, and cultural group selection can result in a special kind of genetic assimilation, in favor of group solidarity.

In short: A cultural regime is evolutionarily discordant if sets up selection pressures against those who keep the regime going. It is concordant if it does the opposite. Within the limits set by enforcement costs, the combination of cultural group selection and genic within-group selection favors solidary, concordant groups. This combination we can call *ethnic group selection*. The greater the contribution of genetic assimilation to the success of a culture, the greater the "ethnic" component to cultural group selection.

3.3. Recruitment

Apart from selection, another process that can change gene frequencies is migration (Rogers, 1990). In some group selection models, migration is highly inimical to altruism. Even extremely low rates of migration – the successful emigration, from a group containing non-altruists, of more than one non-altruist individual over the whole lifetime of the group – can be enough to eliminate altruist genes. This implies that group selection rarely favors the evolution of individual altruism. But the consequences of migration are different when cultural group selection and socially enforced cooperation are involved.

In the case of cultural transmission, the equivalent of migration involves not just physical transfers between groups, but *recruitment*. A group may expand by taking in new members who adopt the local culture. At the same time, the recruitment of outsiders can change a group's genetic composition.

Let's return to our elementary model, a collection of groups under regimes U and V. The frequency of P, a concordant high-solidarity gene, in U is p. A U group recruits members from other groups, including some V groups. The frequency of allele P among these recruits is $p_m = 1 - q_m$. In this case, the equilibrium u, for $u > 0$ is given by:

$$\hat{u} \approx 1 - \frac{g + p_d(f-g)m/s_p}{s_u + m} \tag{9}$$

There are two new variables here, $p_{d.}$ and m. The variable $p_{d.}$ measures the deficit in P among recruits compared to group members, $\mathrm{p_d} = 1 - \mathrm{p_m/p}$. The value of $p_{d.}$ depends on the frequency of U and V groups, and on the frequency of P and Q under each regime, which can be calculated numerically for particular cases.

The variable m is the fraction of the membership of a U group that is recruited from outside in each generation. The variable shows up twice in the equation. In the denominator, m shows up along with s_u, indicating that a group can grow both by natural increase (biological reproduction, the s_u term) and by recruitment (social reproduction, the m term). The variable m also shows up in the numerator, indicating that gene flow from outside increases the rate of U-to-V defection. This effect is stronger if $p_{d.}(f - g)$ is large, so that recruits have a high frequency of Q alleles and/or Q raises defection rates a lot. The effect is also stronger if $\mathrm{s_{p.}}$ is small, so that within-group selection is not very effective in removing the Q alleles introduced by recruitment.

The double role of m in Condition (9) implies that recruitment entails another fecundity/fidelity tradeoff. Recruitment increases the (cultural) fecundity of groups, but reduces the fidelity with which culture is transmitted to the next generation. The break-even point, where $d\hat{u}/dm = 0$, is given by $g/s_u = p_{d.}(f - g) / s_p$. Below this point, an increase in m means an increase in equilibrium u. Above this point, an increase in m means a decrease in equilibrium u. The critical point marks the dividing line between two selective domains:

$$\frac{g}{s_u} > \frac{p_d(f-g)}{s_p} \quad \text{Open} \tag{10}$$

$$\frac{g}{s_u} < \frac{p_d(f-g)}{s_p} \quad \text{Closed} \tag{11}$$

In the preceding subsection, we saw that selection among and within groups combined – ethnic group selection – can favor solidary concordant groups. In this subsection, we encountered two more variables, $p_{d.}$ and m, that ethnic group selection might act on. Either variable could be under group control, and might be dialed up or down to promote group reproduction, although, as before, we must allow for enforcement costs and other tradeoffs. First, a group might change $p_{d.}$, by changing its *sources* of recruitment. Other things being equal, groups that minimize p_d will be most successful. Second, a group might change, m, its *rate* of recruitment. This variable plays an equivocal role. In the open domain, the most successful groups produce as many cultural offspring as possible, by a combination of natural increase and the recruitment of outsiders. In the closed domain, the most successful groups expand through natural increase, and avoid recruiting outsiders, who raise the probability of defection.

3.4. The problem of altruism

We turn from migration to another area where the genetic makeup of groups makes a difference.

Cultural group selection can favor group cooperation, where all group members pay the cost of a public good and all benefit. But it can also favor socially enforced altruism, directed from one group to another. (We already met with socially enforced altruism above, in the form of socially enforced nepotism in small kin groups.) Considered at the individual level, socially enforced altruism doesn't look like altruism: a helper is motivated by social rewards and punishments rather than by altruistic sentiments toward recipients. Considered at the group level, however, socially enforced altruism really is altruism: a group is pushing its members to pay a fitness cost to help members of another group. Socially enforced altruism between groups – whether ethnic groups or kin groups – is the group analog of altruism between individuals.

Imagine once more a population subdivided into groups. Sometimes opportunities arise for one group to help another, with the helping group paying a fitness cost c to provide a benefit b for the recipient group. (These are total costs and benefits, not costs and benefits per capita.) This might involve the donor group inviting the recipient group to share in its common property. Or the donor group might enforce a moral code that rewards its members for acts of kindness to members of the recipient group. Or the donor group might ally militarily with the recipient group, instead of with a culturally unaffiliated group. As before, each group belongs to one of two cultural regimes, U or V. In this case, U groups help other, needy U groups when the opportunity arises, while V groups provide no assistance. In the simple gene-free case, regime U is favored by cultural group selection as long as $b > c$, so that u increases up to the point that selection is balanced by defection.

For this to work, altruism must be discriminating: U groups must direct assistance selectively to other U groups, rather than to V groups. This in turn poses the problem of how one U group recognizes another. One possibility is that a group which is known to have helped other U groups in the past is recognized as a U group in good standing, and deemed worthy of assistance when in need. This makes altruism between groups a multi-generation, group-level version of *indirect reciprocity* (Leimar & Hammerstein, 2001; Nowak & Sigmund, 1998). Briefly, indirect reciprocity is an extension of direct reciprocity. In direct reciprocity, you help those who have helped you. In indirect reciprocity, you maintain a reputation as someone deserving of help by helping others who are deserving of help. Both theoretical and empirical work has demonstrated that indirect reciprocity can operate between individuals. If we accept that a group can impose a code of conduct on its members, then indirect reciprocity among groups is a logical extension of indirect reciprocity among individuals. But so far this is not much like kin altruism. Groups help other groups with similar phenotypes – helpers help helpers – not similar genotypes.

Suppose, however, we again add genes to the model, in the form of alleles P and Q, with P being positively selected within U and, concordantly, lowering the rate of defection from U. Let different U groups have different frequencies of P and Q. Then they also have different likelihoods of leaving descendant U groups, according to:

$$w_i = p_i^{(f-g)/s_p} \tag{12}$$

(See Appendix.) Here w_i is proportional to the expected long-term number of descendant U groups produced by group i, where i is in regime U and has a frequency of P equal to p_i. If p_i is high, then so is w_i,

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and group *i* will lose fewer descendants through defection, and contribute more descendant groups to future generations, than a group with low *p*.

This in turn has implications for the evolution of socially enforced altruism between groups. Whether group *j* should pay cost c_j to provide benefit b_i to group *i* (where both groups are in regime U) will depend on w_i and w_j, according to

$$c_j/b_i < r_E^{(f-g)/s_p} \equiv w_i/w_j \tag{13}$$

where $r_E = p_i \,/\, p_j$.

Condition (13) looks something like Condition (1), the version of Hamilton's rule given near the beginning of this article. We can compare two kinds of altruism, individual altruism resulting from kin selection, and socially enforced altruism resulting from ethnic group selection, by comparing these conditions.

According to the kin selection condition, the "value" of one individual to another is the product of two components, r_{ij} and v_{ii}/v_j. There is a separation of variables here, between the coefficient of relatedness and the ratio of reproductive values. This separation is possible because the coefficient of relatedness of *i* to *j* depends on their genealogical past, while the reproductive values of *i* and *j* depend on their expected reproductive futures, as determined by life history variables like age.

In contrast, in Condition (13) the "value" of group *i* to group *j* is folded into a single component, expressed in terms of either r_E or w_i/w_j. We can call r_E the *ethnic coefficient of relatedness*. Like other *r*'s, it is a regression coefficient, the ratio of expected numbers of altruism genes in recipient and donor$_j$. Alternatively, the ratio w_i/w_j. is comparable to the ratio of reproductive values in Condition (1). The equivalent r_E and w_i/w_j terms look both to the past – because the genetic makeup of a group depends on its history – and to the future – because the genetic makeup of a group, evolving over time depending on $(f - g) \,/\, s_p$., determines the fidelity of cultural transmission. This has no parallel in the kin selection case, where the mutation rate is assumed to be negligible, and in any case doesn't vary with *r*.

Another important contrast between kin selection and ethnic group selection shows up if we think about p_i and p_j in Condition (12). Both kinds of selection depend on groups being genetically different at loci involved in altruism. But the evolutionary forces that generate group differences are not the same. With kin selection, between-group differences result from random variation in gene frequencies between families. But with ethnic group selection, between-group differences in *p* may result from a variety of evolutionary processes. Random genetic drift is one of these, but in large long-lasting groups, selection and migration can be more important.

And this in turn entails a further contrast between kin selection and ethnic group selection: because the sources of genetic variation among groups are different in the two cases, the cues to relatedness will be different as well. Specifically, with ethnic group selection, some of the important cues may involve a group's history of selection and recruitment. For example, selection may result in groups with the same "phenotype" (belonging to the same cultural regime) having very different "genotypes" (different gene frequencies). The length of time a group has spent in a regime is a cue to its genotype. A group in regime U can figure out the frequency of P in another U group if it knows how long the other group has been in regime U, according to the formula:

$$p[t] = \frac{p_0 \cdot e^{s_p \cdot t}}{1 - p_0 + p_0 \cdot e^{s_p \cdot t}} \tag{14}$$

where *t* is the time spent in regime U, and p_0 is the frequency of P when a group first switches from V to U. Altruism toward the other group can then be modulated accordingly.

This example could obviously be elaborated. For example, we could explore cues involving different histories of recruitment. Or we could investigate the indirect route to cultural/genetic reproduction that occurs if defecting U groups, by "seeding" regime V with altruism genes, increase the rate of counter-defection from V to U.

Here, however, we keep things simple, in order to focus on comparing kin selection and ethnic group selection. Up to this point, the comparison has emphasized how they differ; ethnic group selection is *not* kin selection. Yet the two processes also share important similarities. Both involve more than just self-interested cooperation; they are about altruism based on shared genes. More generally, as a result of ethnic group selection, members of ethnic groups may act jointly to regulate sources and rates of group recruitment, and to help fellow ethnics, guided by cues to ethnic group genetic relatedness. This would involve group members establishing and enforcing norms and institutions. I suggest we might reasonably call this *ethnic nepotism*.

4. Ethnicity and evidence

There is one further difference between kin selection and ethnic group selection. Genetic similarity within families – the basic requirement for kin selection – follows automatically from the way sexual reproduction works. By contrast, genetic similarity within ethnic groups at relevant loci – the basic requirement for ethnic group selection – depends on special conditions that might or might not have held in the evolutionary past. So ethnic group selection is an iffier proposition than kin selection. Below we consider whether it is a realistic possibility, in light of several lines of evidence. The discussion is necessarily brief. Other important lines of evidence, including work in political science and history on ethnicity and ethnonationalism, must be left for another occasion.

4.1. Population genetics and population replacement

In the model developed here, some ethnic groups replace others. Group replacement may explain some puzzling features of human

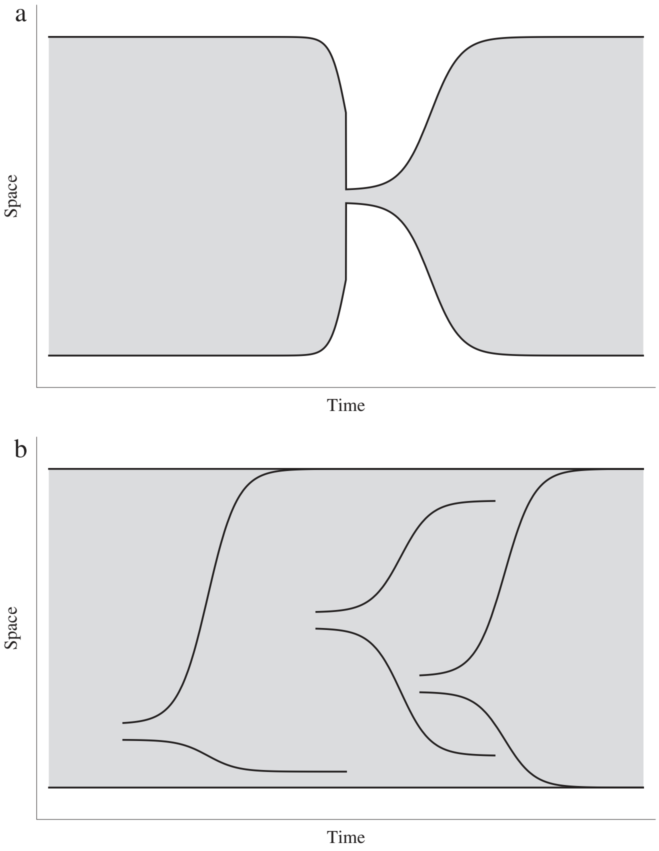

Fig. 1. a. Population bottleneck. b. Population replacement.

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population genetics (Premo & Hublin, 2009). Humans display less genetic diversity than chimpanzees or gorillas; the past effective population size for humans (around 10^4) is considerably smaller than for great apes. This is odd, because humans have had a greater geographic range, and probably higher total population, for some time.

The usual interpretation of this finding is that human beings passed through a bottleneck in which total population was small (Fig. 1.a). In the most dramatic bottleneck scenario, humanity came close to extinction with the Toba volcanic eruption 74,000 years ago, and rebounded from a small population of survivors (Ambrose, 1998).

There are problems with any model involving a population bottleneck (Harpending et al., 1998). Different genetic loci give inconsistent estimates of effective population sizes and timing of bottlenecks. Furthermore, small effective population sizes are characteristic not only of modern humans, but of Neanderthals, and human ancestors going back 500,000 years. Several authors propose an alternative: population replacement associated with cultural group selection. In this hypothesis, total human population is always large. However effective population size is small because a small fraction of groups expand, replace others, and contribute most of the ancestry of later populations (Fig. 1.b).

Whitehead, Richerson, & Boyd, 2002) conduct a simulation of gene/culture coevolution, and show that with (a) low rates of migration between groups, (b) substantial fitness variation associated with cultural differences, and (c) low rates of cultural transmission between groups, the "cultural hitchhiking" of genes associated with successful cultures can produce low effective population sizes, in agreement with the genetic record. Premo and Hublin (2009) find similar results in a model of *culturally mediated migration*, "the general mechanism whereby individuals can only migrate to groups that surpass a given level of cultural familiarity" (p. 33). In their model, genes don't just hitchhike on cultural expansion, but may drive it.

These authors don't specify the nature of the fitness advantage associated with different cultures. Archeologists, if they allow at all for differential cultural success and population replacement, commonly favor materialist explanations, like environmental change or differences in technology. For example, a popular explanation for population replacement in the Holocene involves the spread of agriculture (Bellwood, 2005). Farming can support more people per square kilometer than foraging, and farmers tend to expand at the expense of foragers.

But in this case there are indications that the story is more complicated, and involves differences in social organization. The Austronesians, a classic case of a supposed farming expansion, now look more like "an agricultural revolution that failed" (Blench, 2014). Early Austronesian speakers arriving in island Southeast Asia and Melanesia were "fisher-foragers" more than they were farmers, pioneers lighting out for the territory in order to reproduce a hierarchical sacred order. The Bantu, another classic case of supposed First Farmers, apparently showed up in East Africa later than earlier farmers and herders, with a socio-cultural organization that facilitated the assimilation and replacement of earlier arrivals (Ehret, 1998).

More generally, major demic expansions seem to have spread distinctive social structures that did not merely piggyback on new technologies, but helped to propel the expansions (Jones, 2003, 2011). And in historic times, the differential expansion of states and cultures seems to have resulted not just from material advantages, but from differences in the strength of *ultrasocial norms* (Turchin, Currie, Turner, & Gavrilets, 2013). (However in these cases population replacement typically affected elites more than commoners.)

4.2. The ethnocentric complex

The behavior genetic changes associated with a single episode of demic expansion are likely to be modest, but as long as defection rates are not too high, changes can accumulate over time. Eventually an evolutionary history of ethnic group selection should leave its stamp on human psychology.

The psychology of ethnicity and ethnocentrism, according to the model developed here, does not take the form of a uniform ethnicity module or Darwinian algorithm. Instead, because no cultural regime is reproduced perfectly and different regimes impose different selection pressures, there is heritable variation in ethnocentrism. Also, the psychology of ethnocentrism, according to the model, is not simply an individual disposition to help fellow ethnics. It is a *political* psychology, a disposition to maintain a particular social order – a group phenotype – that regulates ethnic group cooperation, recruitment, and altruism.

Compare this with our emerging understanding of political psychology. On current evidence, individuals' political opinions are not just a product of self-interested calculation or rational deliberation. Nor are they just a historically contingent hodgepodge. Instead, opinions largely reflect stable underlying individual variation in attitudes toward social order, hierarchy, tradition, and in-groups and out-groups. These can be ordered roughly along a right-left, conservative-liberal axis (Duckitt, 1989; Hatemi & McDermott, 2012; Hibbing, Smith, & Alford, 2013; Tuschman, 2013). And the variation is heritable (Martin et al., 1986; Smith, Oxley, Hibbing, Alford, & Hibbing, 2011).

For example, one line of research identifies a cluster of political views that has been labeled Right Wing Authoritarianism (RWA) (Altemeyer, 1996). RWA has three components, authoritarian submission, authoritarian aggression, and conventionalism. RWA is a stable individual disposition. And measures of RWA are valid across cultures, although some of the associated policy particulars vary (de Regt, Mortelmans, & Smits, 2011).

Related work by Haidt and coworkers (Graham, Haidt, & Nosek, 2009) points to five psychological systems underlying moral intuitions: avoidance of harm, fairness, hierarchy, groupishness, and sacredness. The first two principles are important both for liberals and conservatives, while the last three operate more strongly among conservatives.

Authoritarianism correlates with ethnocentrism (Altemeyer, 1996; Kinder & Kam, 2009). Research on ethnicity consistently finds a general dimension of prejudice: individuals with negative attitudes about one outgroup usually have negative attitudes about other outgroups. (However, positive attitudes toward one's own group correlate imperfectly with negative attitudes toward outgroups, both across individuals – Kinder & Kam, 2009 – and across cultures – Cashdan, 2001.) Ethnocentric individuals show a higher degree of group identification in experimental settings (Perreault & Bourhis, 2016). Ethnocentrism and stereotype endorsement also correlate with *essentialist* beliefs in the discreteness, immutability, and biological basis of social categories (Haslam, Bastian, Bain, & Kashima, 2006).

And ethnocentrism – measured as the difference between attitudes toward one's own group and toward outgroups – predicts variation in opinions on a number of issues (Kinder & Kam, 2009). For example, in the United States, more ethnocentric whites are more likely to oppose government programs that disproportionately benefit non-whites, but to support broad based programs like Social Security.

In short, there is a heritable syndrome of political attitudes associated with ingroup favoritism and the enforcement of social rules. More tentatively, this syndrome may include essentialist beliefs about social categories. Interestingly, conservative traits form a tighter phenotypic cluster than liberal ones, suggesting that conservatism has been more of a target of selection (Hibbing et al., 2013, pp. 223–224). All this is consistent with the argument here, that ethnic group selection has shaped political psychology. More specifically, that an ethnocentrism syndrome has been maintained because, in some societies at some times, individuals high in ethnocentrism and conservatism have succeeded in setting up social enforcement mechanisms that both favor their group in competition with others and, concordantly (see Subsection 3.2), impose extra costs on non-conforming, non-ethnocentric individuals within the group.

There are other possibilities, of course. It could be that genes "for" political attitudes were selected for something other than their political effects. Consider that political attitudes correlate with pre-political personality traits like openness to experience (correlated with liberalism)

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and conscientiousness (correlated with conservatism). Conceivably the influence of genes on political attitudes might follow the sequence genes → personality → politics, and the real evolutionary story might involve genes and personality, with political attitudes dragged along as a byproduct. But the behavior genetic data show something else; they show a direct connection running from genes to attitudes, independent of personality (Hatemi & Verhulst, 2015; Verhulst, Eaves, & Hatemi, 2011). This suggests we need to think seriously about the co-evolutionary dynamics of genes, political attitudes, and cultural regimes.

5. Conclusion

Both the study of prehistory and political psychology are changing rapidly in the face of new evidence from biology, especially genetics. It would be intellectually satisfying if we could integrate these findings under the heading of an already existing theory, by equating ethnicity with kinship and applying kin selection theory. But we've seen that this won't work. Ethnicity, like kinship, may have to do with shared genes, and there may be such things as ethnic genetic interests and ethnic nepotism. But an evolutionary theory of ethnicity – even the barebones theory presented here – has to be something more than the theory of kin selection, because of the way ethnicity is entangled with some of the most complicated aspects of human sociality: norms, rules, and political ideals, and the way they affect, and are affected by, large-scale population processes.

Appendix A. Derivation of Condition (12), $w_i = {p_i}^{(f-g)/s_p}$

In a group in regime U with an initial frequency of P equal to p_0, the frequency of P will evolve over time according to a logistic equation:

$$p[t] = \frac{p_0 \cdot e^{s_p \cdot t}}{1 - p_0 + p_0 \cdot e^{s_p \cdot t}} \tag{A1}$$

The proportional growth rate for such a group is given by:

$$\frac{u'[t]}{u[t]} = s_U - (f(1-p[t]) + g \cdot p[t]) - z \tag{A2}$$

where z, which is the same for all U and V groups, is set to ensure that the net change in in frequency across all groups sums to 0. Solving for $u[t]$ gives:

$$u[t] = u_0 \cdot e^{(s_u - f - z)t} \left(1 - p_0 + p_0 \cdot e^{s_p \cdot t}\right)^{(f-g)/s_p} \tag{A3}$$

Over a long period of time, the quantity in parentheses is dominated by the $p_0 \cdot e^{S_p \cdot t}$ term, so:

$$u[t] = u_0 \cdot e^{(s_U - g - z)t} \cdot {p_0}^{(f-g)/s_p} \mathrm{ast} \to \infty \tag{A4}$$

We can normalize this by dividing by $u_0 \cdot e^{(S_U - g - z)t}$, the expected long-term increase of a U group that starts out with $u = u_0$ and $p = 1$, to get:

$$w_i = p_i^{(f-g)/s_p} \tag{A5}$$

where w_i is the normalized long-term reproductive contribution of a group in regime U with frequency of allele P equal to p_i. This is Condition (12) in the text.

This derivation assumes a steady state distribution of U and V groups with various p_i, so that z is not a function of t. It ignores the indirect route to cultural/genetic reproduction that occurs if defecting U groups, by "seeding" regime V with P, increase the rate of counter-defection from V to U.

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Please cite this article as: Jones, D., Kin selection and ethnic group selection, *Evolution and Human Behavior* (2017), https://doi.org/10.1016/j.evolhumbehav.2017.08.004

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Please cite this article as: Jones, D., Kin selection and ethnic group selection, *Evolution and Human Behavior* (2017), https://doi.org/10.1016/j.evolhumbehav.2017.08.004