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Group Nepotism and Human Kinship¹

by Doug Jones

The human aptitude for collective action may have implications for how the theory of kin selection applies to human kinship. Several models show that if two or more individuals act collectively in assisting their mutual kin, their effective coefficient of relatedness can be greater than if each acts individually. Thus human beings may have psychological adaptations not only for individual nepotism but also for group nepotism—adaptations leading them to construct solidary groups enforcing an ethic of unidirectional altruism toward kin. Human kinship systems have a number of features that seem especially consistent with group nepotism: (1) Human kin groups come in many sizes, ranging from families to clans, lineages, and tribes of thousands of people. (2) Human kinship commonly features an “axiom of amity,” a presumption that kin are entitled to aid simply by virtue of being kin. But this kin altruism is often socially imposed, motivated less by affection between donors and recipients than by social pressure. (3) Relatedness as defined by human kinship systems often differs systematically from biological relatedness and varies with social structure—especially with the solidarity of the kin group. The theory of group nepotism may have implications for a number of research areas in the social sciences. I conclude by focusing on two: demand sharing of food among subsistence hunters and the psychology of ethnocentrism.

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How much has the theory of kin selection contributed to our understanding of human kinship outside the family? Many early manifestoes in the field of evolution and human behavior argue that there is an affinity between evolutionary biology’s theory of inclusive fitness and social anthropology’s traditional interest in kinship in tribal societies (Wilson 1975, Alexander 1979). These early programmatic statements were followed by a small number of high-quality ethnographic (Chagnon and Irons 1979, Chagnon 1992), cross-cultural (Flinn 1981), and theoretical (Hughes 1988) works on evolution and human kinship. Yet the current situation is perhaps more fairly represented in Ridley’s (1997) recent survey *The Origins of Virtue*, which reviews a wide range of theory and research—including research in tribal societies—on evolution and human “moral instincts.” In this book the theory of inclusive fitness is presented briefly, but mostly to contrast its importance among eusocial insects with its supposed irrelevance to human sociality outside the family (pp. 39–40). And the classic social anthropology of kinship is mentioned not at all.

Some anthropologists consider inclusive fitness theory irrelevant to human kinship because they consider evolutionary theory in general irrelevant to human social behavior (Sahlins 1976, Schneider 1984). But even those sympathetic to evolutionary approaches often argue that inclusive fitness considerations are probably important only among the closest kin (Brown 1991:107):

A problem in the application of kin selection theory to anthropological problems concerns the distance at which kinship ties are calculated. It is not at all clear that humans (or any other species) are adapted to distinguish between degrees of distant kin. . . . What the evidence suggests therefore is that those kinship sentiments constituted by phylogenetic adaptation generally work within a narrow range of kin.

(Hechter [1987:70–71] makes a similar argument.) Because genetic relatedness to distant kin is low and because in any case people who claim kinship with distant relations often seem to be careless about the exact genealogical connections involved, it might seem reasonable to argue that the theory of kin selection, according to which altruism—measured as the ratio of costs to donor and benefits to recipient—should be proportional to genetic relatedness, is not directly relevant to understanding human kinship much beyond the level of the extended family. At best the theory might be indirectly relevant: for example, feelings of attachment to parents, siblings, and other close kin might be evoked secondarily and symbolically in mobilizing larger groups.

In this paper, however, I will argue that the scope of the theory of kin selection may be greatly expanded if we allow for the possibility of *group nepotism*—assistance to kin carried out by groups rather than individuals. When altruism toward kin is a group enterprise, socially imposed, it may be adaptive for members of large groups to provide unreciprocated assistance to

their mutual kin over and above the level that would be adaptive for individuals acting on their own. At the same time, group nepotism makes kinship partly a matter of social definition, because the willingness of one individual to treat another as a kinsman depends on the inclinations and powers of other group members.

In the first section of this paper I take up the general problem of the evolution of collective action, arguing that human beings are likely to have evolved psychological mechanisms—"moral sentiments"—adapted to solving collective action problems. In the second section and in an appendix I consider the population genetics of group nepotism, deriving several versions of the coefficient of relatedness for group kinship. In the third section I consider some features of human kinship systems that seem to be more consistent with group nepotism than with egoism or individual nepotism. In two final sections I take up the possible role of group nepotism in the demand sharing of food among subsistence hunters and in ethnocentrism and ethnonationalism.

Collective Action and Moral Sentiments

One of the distinguishing features of human beings is an extraordinary capacity for collective action—for the construction of collective actors, including clans, lineages, tribes, corporations, guilds, sects, political movements, and states, which may act as vehicles of group interests. Edward O. Wilson (1975:380) notes that this capacity places human beings at one of the "pinnacles of social evolution," sometimes approaching social insects in level of cooperativeness and far exceeding them in flexibility.

Collective action is rare among nonhuman animals and problematic even among humans in part because the existence of groups with common interests does not automatically result in collective action in pursuit of those interests, owing to the problem of "free-riding" (Olson 1965). In the classic formulation of this problem, individuals can make some contribution toward a public good. The cost of a contribution is borne separately by each individual, while the benefits are shared by all, including noncontributors. Individuals who benefit from the contributions of others while making no contribution of their own are known as "free-riders." In a typical public-goods situation, free-riders do better (have higher utility or greater fitness) than non-free-riders, so that free-riding is a dominant strategy. However, if all individuals are free-riders, then all individuals are worse off than they would be if all contributed. The individual pursuit of self-interest leads to a collectively bad outcome. Thus, in a public-goods situation, there may be a potential gain for all individuals if a social contract can be devised to exact a contribution from everyone through "mutual coercion, mutually agreed upon" (Hardin 1968).

To enforce a social contract, individuals must reward and punish others not merely to the extent that their own immediate interests are involved but also according to how the behavior of others conforms to group norms

of honorable, moral, legal, or otherwise acceptable behavior. Because the punishment of free-riders is a public good in its own right, individuals must also punish those who fail to do their part in punishing free-riders. Thus the ability to enforce collective sanctions depends on the ability both to monitor individual contributions and to apply "selective incentives" to free-riders—either directly punishing them or excluding them from jointly produced goods. And this depends in turn on the ability to sanction agents who will take on the responsibility for monitoring and sanctioning behavior. In small groups with informal controls, every adult may act as an enforcer; in large groups, the role of enforcer may fall to specialists. Whatever the group size, the level of group solidarity depends not only on the extent of common interests but also on the ability to detect and punish free-riding (Hechter 1987).

Even where the means exist to enforce compliance with group norms, there is still a question of whether the norms enforced will be beneficial to the group enforcing them. Boyd and Richerson (1990a) point out that nothing in the formal logic of public-goods theories guarantees that groups with the means to enforce collective norms will enforce norms which contribute to collective well-being. Given a group in which individuals are rewarded for doing X (assuming that the reward exceeds the cost of doing X) and rewarded for rewarding those who do X (assuming again that rewards exceed costs), and so on, recursively, it will be advantageous for individuals to do X, even if X is neutral or even harmful to group well-being. Elsewhere, Boyd and Richerson (1990b) suggest that one way around this problem, at least on evolutionary time scales, involves taking selection between groups into account. If different groups enforce different collective values, then those groups enforcing group-beneficial values will out-reproduce those enforcing group-detrimental values. The resulting process can be described as a form of group selection, but in contrast to more familiar models of group selection it does not require any "altruism" on the part of individuals. Instead it involves selection between groups at alternative evolutionarily stable states. Taking the argument a step farther, groups whose members discuss group norms and revise rules that are harmful to group fitness may out-reproduce groups that avoid such changes (Boehm 1996). Whether the evolution of adaptations for collective action necessarily or typically involves group selection is a matter of dispute—and of definition (Alexander 1987, Wilson and Sober 1994). For purposes of this paper, the important point is that collective action is such a special feature of the evolutionary landscape that controls imposed on individuals in the course of constructing collective actors are properly distinguished from other outside influences on behavior.

What distinctive features of human psychology account for the aptitude for collective action? A number of researchers have argued in recent years that the human psyche comprises not a unitary capacity for culture but a large number of distinct "mental organs" each specialized to perform a certain range of cognitive tasks

(Barkow, Cosmides, and Tooby 1992, Hirschfeld and Gelman 1994, Jones 1999). As Atran (1993:66) has put it,

The claim . . . is that some abilities, concepts, and beliefs are easily acquired, without the help of instruction (formal or informal) aimed at “socialization” or “enculturation,” and on the basis of ordinary interactions with others and the environment. What makes this acquisition easy is an innate readiness that takes different forms for different domains, or, in other terms, a set of domain-specific cerebral dispositions.

Problems of collective action are a good candidate for a specialized domain of reasoning and motivation (Cosmides and Tooby 1992). Collective action depends in part on the exercise of language and general planning abilities. But to the extent that problems of collective action have been a recurrent feature of the human evolutionary past, humans are likely to have specialized psychological adaptations to these problems, and contributions to the public good are likely to be the product not merely of rational calculation but of “moral sentiments” regulating each individual’s willingness to contribute and to punish free-riders.

Jackendoff (1994) argues that group psychology has deep evolutionary roots and depends on innate mental models. “In some species, especially primates, . . . the group is not just a convenient aggregate of individuals, but a semi-permanent collection of individuals who know each other. . . . Any individual of the species will be recognized by group members as ‘in the group’ or ‘out of the group’” (pp. 212–13). According to Jackendoff (p. 215), human beings have added a normative dimension to this primate heritage:

The social group is . . . the unit over which we define *codes of conduct*. . . . The code gives the group (or its authority figures) the license to punish (or otherwise sanction) a group member who engages in undesirable or impermissible behavior. Part of the “social contract” is that if we admit to doing something wrong, we thereby acknowledge that it’s acceptable for the group to punish us. . . . Of course, part of “learning” a particular culture or subculture is learning the details of its code of conduct. But we don’t have to learn *that there is such a thing as a code of conduct*. The concept of a code of conduct associated with a group is [one] of these skeletal notions around which we structure our social existence.

In conclusion, the human capacity for culture may be not one faculty but many, involving the operation of a large number of distinct psychological mechanisms shaped by natural selection to solve particular adaptive problems. These mechanisms may include moral sentiments adapted to solve collective action problems—to facilitate the construction of collective actors. If, as I will

argue in the next section, the theory of kin selection looks different when we include the possibility of collective assistance toward kin, then it may be reasonable to look for moral sentiments adapted for group nepotism in humans. The rest of this paper will explore this possibility.

Models of Group Nepotism

In the classic formulation of kin selection, an individual has the option of reducing his or her own fitness to help a relative. If $B/C > 1/r$ —if the relative’s expected fitness gain (B) divided by the helper’s expected fitness loss (C) is greater than the reciprocal ($1/r$) of the coefficient of relatedness—then, other things being equal, a gene making kin altruism more likely will be favored by natural selection. This inequality is known as Hamilton’s Rule (Hamilton 1964). Given certain assumptions about the genetics of the situation, the decision to help or not to help can be treated as an optimization problem: the most adaptive behavior will be that which maximizes inclusive fitness.

In this section I consider a different problem. I take it as given that people at least sometimes overcome the problems of acting collectively in the face of free-rider problems and ask how altruistic a group of two or more individuals should be when acting together to help one or more of their mutual kin. In this case, inclusive fitness theory doesn’t always give the correct answers, because the assumptions made in deriving the theory don’t always hold. Instead, models with explicit population genetics are needed. I present several such models below.

MODEL I: CONDITIONAL NEPOTISM AND THE BROTHERS KARAMAZOV GAME

The simplest case of group nepotism involves two siblings who are in a position to help a third. Eshel and Motro (1988) analyze one version of a “three brothers’ problem,” in which the presence of another potential helper *lowers* the expected level of altruism below that predicted by Hamilton’s Rule because each potential helper is tempted to let the other do most of the helping. Here we are interested in a different version of the problem, in which two siblings, acting together rather than separately, provide a *higher* level of altruism to a third than predicted by Hamilton’s Rule.

Imagine, then, a case involving Dostoevsky’s brothers Karamazov, Dmitri, Ivan, and Alyosha. Suppose that Dmitri often finds himself in need of a helping hand. He turns half the time to Ivan and half the time to Alyosha and is never in a position to reciprocate. According to Hamilton’s Rule and given that the coefficient of relatedness, r , between full siblings is $1/2$, if Ivan decides independently of Alyosha’s past or future decisions to help Dmitri, he will post a net gain in inclusive fitness only if the benefit to Dmitri is more than twice his own cost. The same holds for Alyosha if he decides on his own to help Dmitri. Note, however, that when Ivan helps

Dmitri, he seems to be providing a free genetic benefit to Alyosha, and when Alyosha helps Dmitri, Ivan seems to get a free benefit. Ivan and Alyosha, in other words, seem to be taking turns free-riding on one another.

Can Ivan and Alyosha overcome this apparent free-rider problem by acting in concert? Suppose that Ivan indicates to Alyosha that he is following a strategy of “conditional nepotism”: he will behave more altruistically to Dmitri *if and only if* Alyosha is willing to do the same. Although only a formal population genetic model will give an exact result, inclusive fitness theory provides qualitative insight. Ivan is proposing a package deal in which he provides benefit B to Dmitri at cost C to himself and 0 to Alyosha on one round, while on the next round Alyosha provides a further benefit B to Dmitri at cost C to himself and 0 to Ivan. Adding up Ivan’s inclusive fitness costs and benefits, we get $B/C > 3/2$. In other words, this argument suggests that it would be adaptive for Ivan to treat Dmitri *as if* their coefficient of relatedness were $2/3$ rather than $1/2$, provided that Alyosha was willing to do the same.

For a more accurate answer, consider the fate of a gene for conditional nepotism. Suppose that in a population of trios of brothers there are two types of nepotists, Hamiltonian nepotists and conditional nepotists. If either Ivan or Alyosha is a Hamiltonian nepotist, they will not cooperate with one another in helping Dmitri: instead each will assist Dmitri only as long as Dmitri’s benefit is more than twice his own cost. But if both Ivan and Alyosha are conditional nepotists, the threshold for nepotism will be lower: each will assist Dmitri as long as the benefit to Dmitri is more than $1/r_c$ times the cost to each, where r_c is the “conditional coefficient of relatedness,” the effective coefficient of relatedness when brothers act in concert rather than independently. We are interested in the conditions under which conditional nepotists with $r_c > 1/2$ have higher fitness than Hamiltonian nepotists. In a diploid outbred population, an allele coding for conditional nepotism will be favored by natural selection as long as $B/C > 1/r_c$, where

$$r_c = (1 + 6p)/(2 + 8p), \quad (1)$$

with p being the frequency of the allele. This equation assumes that heterozygotes adopt a conditional nepotist strategy with probability $1/2$ and a Hamiltonian nepotist strategy with probability $1/2$ (see appendix for details).

Equation 1 implies that the fate of a conditional nepotism allele will depend on its frequency. If $p = 0$, then $r_c = 1/2$, which means that a single conditional nepotism gene with $r_c > 1/2$ will not be able to invade a large population of Hamiltonian nepotists. But if $p = 1$, then $r_c = 7/10$, which means that a large population of conditional nepotists will be resistant to invasion by a single Hamiltonian nepotist gene as long as $B/C > 10/7$. Alternatively, if conditional nepotists are established in one part of a species’s range and Hamiltonian nepotists in another part, then, in a hybrid zone consisting of equal numbers of the two types ($p = 1/2$), conditional nepotists will replace Hamiltonian nepotists as long as $B/C > 3/2$

(i.e., $r_c = 2/3$). In other words, it will be difficult for conditional nepotists to gain an initial foothold in a population, but once established conditional nepotism can be evolutionarily stable in the face of Hamiltonian nepotism. Similar frequency dependence is found in other models of the evolution of reciprocity (Axelrod 1984); these similarities are explored further in the appendix, where it is shown that conditional nepotism can be modeled as a strategy in a repeated prisoner’s dilemma game.

Because conditional nepotism with an effective coefficient of relatedness greater than $1/2$ can be evolutionarily stable, it can be adaptive for Ivan to treat Dmitri as even closer kin than a brother, provided that Alyosha is willing to do the same. This example demonstrates the principle that whenever more than one individual has the power to help a given relative or relatives, kin altruism is a public good, and the effective coefficient of relatedness may be greater if potential altruists work together.

MODEL 2: COLLECTIVE CHOICE AND SOCIALLY IMPOSED NEPOTISM

In the model above, group nepotism is based on reciprocity. Faced with a Hamiltonian nepotist, a conditional nepotist avoids making any extra contribution to kin rather than trying to coerce an extra contribution from the other party. An alternative to conditional nepotism is socially imposed nepotism, involving “mutual coercion, mutually agreed upon.” When the number of decision makers is greater than two, each individual will be outnumbered by the rest of the group, and the balance of power will be in favor of group members trying to impose agreed-upon norms on the individual, provided that the group has the resources to monitor and sanction conformity to the rules.

Suppose that a group of relatives (the donor group) numbering n_1 faces the choice of whether to help another group of relatives (the recipient group) numbering n_2 . Suppose that the expected coefficient of relatedness between two randomly selected members of the donor groups is r_{11} and the expected coefficient of relatedness between a randomly selected donor and a randomly selected recipient is r_{12} . Suppose that there is sufficient solidarity among donors to exact a contribution from each which will be used to help recipients, with the amount of the contribution determined by a consensus of donors. Equivalently, imagine that donors are deciding whether to *refrain* from a collective project that would help them but injure recipients. It can be shown (given some additional assumptions discussed in the appendix) that an allele leading an individual to support a collective contribution in which each donor benefits each recipient by an amount B , at a cost C , will increase in frequency as long as $B/C > 1/r_g$, where

$$r_g = \frac{n_1 r_{12}}{1 + r_{11}(n_1 - 1)}. \quad (2)$$

The r_g term in equation 2 is the “group coefficient of relatedness”: the relatedness of one group to another group or to an individual. This coefficient determines the threshold for nepotism when members of a group act together.² It is different from—and normally greater than— r_{12} , the average coefficient of relatedness between individuals in the two groups, which determines the threshold for nepotism when members of a group act independently.

An informal inclusive fitness argument may give some insight into r_g . Suppose that we ask a random donor how much of a contribution donors should make to recipients and suppose that the donor’s answer will be based on his or her inclusive fitness costs and benefits, assuming an equal contribution from all donors. The inclusive fitness *benefits* to a random donor are the benefits that donor confers on the average recipient times the number of donors (since other donors also contribute to the average recipient) times the donor’s relatedness to the average recipient: Bn_1r_{12} . The inclusive fitness *costs* are the cost to the donor plus the product of the costs to the other donors, their relatedness to the randomly selected donor, and the number of other donors: $C(1 + r_{11}(n_1 - 1))$. Solving for $B/C > 1$ gives equation 2. To derive this equation more formally we must assume a specific rule of collective decision making (proportional rule; see appendix). For several other collective decision rules, numerical simulations show that equation 2 gives approximately the right answers, although with supermajority rule, where group nepotism only gets off the ground when supported by substantially more than half the group, there is significant frequency dependence: group nepotism is somewhat harder to start up and easier to keep going. A rule of unanimity, as in the Brothers Karamazov game, is a limiting case of supermajority rule. For extreme values of n_1r_{11} equation 2 can be approximately simplified:

$$r_g \approx n_1r_{12} \text{ for } n_1r_{11} \ll 1, \tag{2a}$$

and

$$r_g \approx r_{12}/r_{11} \text{ for } n_1r_{11} \gg 1. \tag{2b}$$

Equation 2 implies that even when average coefficients of relatedness between donors and recipients are low, there may still be considerable potential for group nepotism, provided that donor populations are large and donors are not a lot more related to one another than to recipients. If donors and recipients are members of two distinct but related kin groups, group nepotism may be adaptive even when no donor is closely related to any

recipient. If donors and recipients are affluent and needy members of a single kin group, some donors will be closely related to some recipients, and a significant degree of individual nepotism will be adaptive, but there will still commonly be an additional inclusive fitness payoff from pooling nepotism.

One limitation of group nepotism in this model needs to be stressed: the selective advantage of genes for group nepotism will commonly be lower than for genes for individual nepotism. A gene coding for group nepotism will have a selective advantage of $(B - C/r_g)D$ where $D \approx r_{12}(n_1 + n_2)/2n_1$. In other words, the strength of selection for group nepotistic genes is proportional to r_{12} rather than r_g . Genes for group nepotism will spread more slowly than genes for individual nepotism and will be more subject to drift and pleiotropic effects. This does *not* imply that only low levels of group nepotism will be favored by natural selection, but it does imply that adaptations for group nepotism may not be as finely tuned or as sensitive to exact coefficients of relatedness as adaptations for individual nepotism and that group nepotism in large groups of distant relations may be something of a by-product of adaptations for group nepotism in smaller and more closely related groups. Below I consider a model not subject to these limitations.

MODEL 3: RELATEDNESS THROUGH SHARED SELECTIVE HISTORY

In the preceding model, the coefficients of relatedness, r_{11} and r_{12} , are given as fixed parameters. Alternatively, however, coefficients of relatedness might be treated as variables. More specifically, selection acting within groups might reduce or increase within-group genetic similarity at loci influencing group nepotism. Below I consider how the potential for group nepotism may be either reduced—when selection within groups acts consistently for or against supporters of group nepotism—or increased—when within-group selection acts against supporters of group nepotism in some groups and in favor of supporters in others.

Suppose that we relax the assumption that supporters and opponents of group nepotism pay the same costs. Let S , the “coefficient of solidarity,” be a measure of the relative contributions of supporters and opponents of group nepotism: supporters’ costs exceed opponents’ costs by $C(1 - S)$. In this case the threshold for nepotism is given by

$$B/C > (1 - S)/r_{12} + S/r_g. \tag{3}$$

This inequality implies that when groups make collective decisions, the threshold for nepotism depends both on individual and group relatedness and on the level of group solidarity. When $S = 0$, supporters of group nepotism are unable to extract any contribution from opponents, and inequality 3 reduces to the formula for individual nepotism, $B/C > 1/r_{12}$. When $S = 1$, supporters and opponents make equal contributions, and inequality 3 reduces to the formula for group nepotism, $B/C > 1/$

2. This version of the group coefficient of relatedness is expressed in terms of the costs and benefits incurred by a single donor in assisting a single recipient. This is identical to the group coefficient of relatedness expressed in terms of the total costs and benefits incurred by all donors and recipients. To express the coefficient of relatedness in terms of total costs paid by a single donor and total benefits received by a single recipient we must multiply r_g from equation 2 by n_2/n_1 .

r_g . When $S > 1$, the opponents of group nepotism bear a disproportionate share of the costs. This will be the case if, for example, opponents are particularly likely to be punished for evading their obligations to kin.

One might argue that whenever there is appreciable group nepotism the coefficient of solidarity will be close to 1, because supporters and opponents of group nepotism are likely to adapt to one another's presence: supporters by giving up on group nepotism when there is little prospect of opponents' being made to contribute equal shares, opponents by going along with programs of group nepotism when punishment for noncontribution is more costly than contribution. In other words, group nepotism is likely to take the form of a conditional strategy, with adaptations for group nepotism activated when potential group solidarity is high ($S \geq 1$) but not otherwise. However, even if coefficients of solidarity are close to 1, they are unlikely to be exactly 1. Nonunitary coefficients of solidarity complicate the modeling of group nepotism: for a given coefficient of solidarity significantly less or greater than 1, selection for group nepotism—the S/r_g term—may be swamped by selection for conformity to local norms—the $(1-S)/r_{12}$ term—at least if donors and recipients are not closely related ($r_{12} \ll 1$).

The analysis up to this point suggests that within-group selection will reduce the potential for group nepotism, but this is true only if there is a single populationwide S value. Suppose, however, that groups differ in their coefficients of solidarity and these differences persist over generations. In some groups, a pro-group-nepotism regime prevails: supporters of group nepotism manage to impose a rule of group nepotism which is disproportionately costly to opponents ($S > 1$). In other groups, an anti-group-nepotism regime prevails: supporters do not succeed in imposing any rule of group nepotism and even suffer a selective disadvantage. Within each group, selection favors whichever type is politically dominant, resulting in divergences in gene frequencies between groups and increasing relatedness within them; at the same time, pro groups increase their representation in the population as a whole by practicing group nepotism.

Now suppose that we allow for movement between regimes. In each generation a fraction of individuals and groups get fed up with living under a pro-group-nepotism regime and switch to anti, and vice versa; the probabilities of switching regimes depend on the frequency of group nepotism alleles in a group. In a collection of groups with a low frequency of group nepotism alleles, groups will switch very readily from pro to anti but not very readily from anti to pro, that is, most groups in the collection will not enforce a rule of group nepotism and will provide an unfavorable environment for supporters of group nepotism. By contrast, in a collection of groups with a high frequency of group nepotism alleles, most groups will enforce a rule of group nepotism and make life more difficult for opponents of group nepotism.

Imagine a population with a low frequency of group nepotism genes. Most groups in this population will be in the anti regime, but occasionally a group will switch

to pro. In most cases it will soon switch back to anti, but occasionally it will stick with pro long enough for group nepotism genes to increase in frequency. If this continues for long enough, a balance will eventually be struck between selection within the pro group, which will increase the group's frequency of group nepotism genes, and immigration from anti groups (most of the population), which will reduce it. The equilibrium frequency of group nepotism genes in a pro group greatly outnumbered by anti groups will be

$$p^* \approx 1 - m_1[0]/s \text{ for } s > m_1[0], 0 \text{ for } s \leq m_1[0], \quad (4)$$

where $s = (S-1)n_1/(n_1 + n_2 - CSn_1 + Bn_2)$ is the strength of within-group selection in the pro group and $m_1[0]$ is the rate of immigration from anti groups, which are assumed to have near-zero frequencies of group nepotism genes. Pro groups will increase their representation in the next generation, and group nepotism genes will increase in frequency in the population as a whole, as long as

$$B - C > m_E[p^*], \quad (5)$$

where $B - C$ is the difference between benefits of group nepotism to recipients and costs to donors, measured as in model 2 (see n. 1), and $m_E[p]$, a decreasing function of p , is the rate at which pro groups with a frequency p of group nepotism genes switch to the anti regime.

While the discussion above does not provide a full-blown analytic treatment, equations 4 and 5 do imply two general conditions for the initial spread of group nepotistic regimes and genes. First, selection within pro-group-nepotism groups must outweigh immigration so that such groups can maintain significant genetic differences from their anti-group-nepotism neighbors. Second, this buildup of group nepotism genes must reduce pro groups' rate of defection to the anti regime to less than $B - C$, the between-group selective advantage of group nepotism. Note that in this case it is the *difference* between benefits and costs that matters, not their ratio.

In many models of kin selection, including models 1 and 2 above, members of kin groups share genes as a result of descent from common ancestors, and selection is assumed to cause little change in gene frequencies between the time a gene resides in a common ancestor and the moment it is expressed in his or her descendants. In model 3, by contrast, genetic similarity between descent group members is the product not of common ancestry but of a shared history of selection; the degree of genetic similarity and the potential for socially imposed altruism depend on the balance between migration and selection. In more complex models, both shared ancestry and a shared history of selection might contribute to genetic correlations within descent groups. The important point is that group nepotism may be *autocatalytic*: genes for group nepotism may reinforce their own spread by increasing within-group relatedness at relevant loci so that the potential for group nepotism is greater than

coefficients of relatedness for the genome as a whole would suggest.

Finally, one point worth noting about all of the models above is that they concentrate exclusively on the “*r*” side of group nepotism—on defining group coefficients of relatedness comparable to the individual coefficient of relatedness. However, there is also a “*B/C*” or “*B – C*” side to group nepotism: those who turn to group nepotism rather than relying on individual nepotism will normally face not only a different effective coefficient of relatedness but also different costs and benefits. Such changes in the benefit/cost side of the equation would have to be considered along with changes in effective coefficients of relatedness in any application of the models to specific cases.

SUMMARY OF MODELS AND PREVIEW OF APPLICATIONS

Altruism toward kin is a public good: every time Alice imposes some genetic cost on herself to provide a greater benefit to her relative Zelda, she is also providing a free indirect genetic benefit to Betty, Cindy, and the rest of Zelda’s kin. I have presented three models demonstrating that Alice, Betty, Cindy, and the rest can have higher effective coefficients of relatedness if they act together rather than separately in assisting their mutual kin. Conditional nepotism, the subject of the first model, is likely to apply best to small family-sized kin groups; in larger groups, the requirement that individuals unanimously agree to a higher level of altruism toward mutual kin is unlikely to be met. The second model, in which altruism toward kin results from “mutual coercion, mutually agreed upon,” is most likely to apply to somewhat larger kin groups, in which the balance of power is in favor of group members trying to impose mutually accepted norms on the individual. The third model, in which punishment of nonaltruists changes gene frequencies, thereby increasing within-group genetic similarity and the potential for group nepotism, is most likely to apply to large endogamous descent groups which last for long enough and have low enough levels of migration for within-group selection to produce significant changes in gene frequencies. All three models suggest that in a species with a well-developed capacity for collective action there may be two distinct modes of nepotism, *individual nepotism* and *group nepotism*.

In the rest of this section, I compare group nepotism with two other processes that can result in group-beneficial behavior—assortative interaction and cultural group selection—and introduce potential applications of the theory of group nepotism.

In all models of group nepotism, some group members collectively impose costs on themselves to provide benefits for others, even when there are no return benefits in the offspring. In all models of group nepotism, genes for group nepotism are favored because of genetic correlations between altruists and beneficiaries. In some models of group nepotism (models 1 and 2) these correlations result from shared ancestry independent of within-group

selection; in other models (model 3) they result from a shared history of selection. In the latter case, genetic correlations at loci affecting group nepotism may be much higher than those at other loci. But these models all require that altruists and beneficiaries are of common descent.

Genetic correlations may result from causes other than common descent. Wilson and Dugatkin (1997) consider models of *assortative interaction*, in which individuals inclined to make especially large contributions to group goods try to associate with similarly inclined individuals and to avoid or expel would-be free-riders. These models differ from group nepotism in two respects. First, they do not require any genetic continuity in group membership from one generation to the next. Second, it is not clear that they provide much basis for selection in favor of unidirectional altruism from one segment of a group to another. The second point follows from the first: in models of assortative interaction, it is not clear where genetic correlations between donors and recipients would come from, because it is not clear how potential donors could detect and banish carriers of “free-rider” alleles among potential recipients as long as the latter were not in a position to reciprocate altruism. In models of group nepotism, by contrast, genetic correlations between donor and recipient segments are ensured by common descent even if recipients cannot reciprocate. Of course, real-world problems of collective action may involve both assortative interaction and group nepotism, with the distribution of benefits to individuals depending partly on a demonstrated willingness to contribute to group goods and partly on common descent.

Cultural group selection—another process that can produce group-beneficial behavior—takes place when groups differ culturally, when these differences persist over time, and when groups that chance to have group-beneficial cultural variants replace other groups. Boyd and Richerson (1985:204–40) provide the most explicit formal model of this process, while Soltis, Boyd, and Richerson (1995) provide relevant data on group extinction rates. With cultural group selection there is no direct selection for genes promoting collective action. Instead, selection favors genes that lead individuals to imitate common behaviors, thereby reducing cultural variance within groups, increasing it between them, and incidentally fostering cultural group selection. The only innate disposition necessary is the disposition to copy whatever cultural variants are locally commonest. Because cultural group selection is a genetically nonadaptive by-product of gene selection within groups in favor of particular social learning rules, it does not depend on genetic variation between groups or on genetic correlations within them, and it does not require any innate dispositions to learn and enforce group-beneficial moral rules, to promote group altruism, or to attend to kinship and descent.³

3. But suppose that we add the possibility of “genetic assimilation” to a model of cultural group selection: within some groups there is genetic selection in favor of individuals who conform especially

Although assortative interaction among nonrelatives and cultural group selection may account for important aspects of human sociality, I suggest that group nepotism provides the best explanation for some of the core principles of human kinship. Without group nepotism, in other words, people might still be social animals, but the domain of kinship and descent would be greatly attenuated. It is not currently possible to prove this claim, but three areas of research—the social anthropology of kinship, the behavioral ecology of demand sharing, and the psychology of ethnocentrism and ethnonationalism—may eventually provide some of the data needed for a real test of the theory of group nepotism, and the theory may in turn shed light on current scholarly debates in these areas.⁴

Group Nepotism and the Social Anthropology of Kinship

Human kinship seems to display a number of features which are hard to square with the common postulate that human action is fundamentally egoistic or individually nepotistic but which follow in a straightforward fashion from the theory of group nepotism:

1. Human kin groups come in many sizes, ranging from families to clans, lineages, and tribes of thousands of people.

2. Human kinship commonly features an “axiom of amity,” a presumption that kin are entitled to aid simply by virtue of being kin, independently of their ability to reciprocate or coerce. However, kinship systems commonly also include a distinction between domestic and jural domains; altruism in the jural domain is socially imposed, motivated less by affection between donors and recipients than by social pressure and a sense of duty.

3. Relatedness as defined by human kinship systems may differ systematically from biological relatedness, and kin categorization is often carried out in ignorance of the exact genealogical connections between the individuals involved; even individuals known to be genealogically unrelated may be accepted as kin.

GROUP KINSHIP AND GROUP SIZE

Human kin groups commonly attain considerable size. Among nonagricultural peoples, kin groups with some degree of solidarity and collective identity often number in the hundreds and sometimes in the thousands. Among

well to group norms, and levels of migration are low enough to allow significant genetic differentiation between groups. In this case we arrive by a different route at a model of group nepotism in which genetic correlations between altruists and beneficiaries are generated by shared selective history (see model 3 above).

4. There are other research areas—for example, the debate between moral economy and political economy theories of peasant societies (Scott 1976, Popkin 1979)—where the theory of group nepotism might also make a contribution, but these must be left for future investigation.

non-state agriculturalists and pastoralists, kin groups may attain populations in the thousands or even tens of thousands. Large well-organized kin groups are also found among some nonhuman clades, including ants, bees, termites, and naked mole rats, but the evolutionary bases of kin-group formation for these clades are very different from those for humans. Among nonhumans, two phenomena—reproductive skew and group endogamy—can produce very high coefficients of relatedness between group members. Among humans coefficients of relatedness are rarely high enough to make individual nepotism adaptive in large kin groups but are often high enough that group nepotism is potentially important.

Reproductive skew (Keller and Reeve 1994), whereby some organisms contribute more to the next generation than others, will increase group coefficients of relatedness. Reproductive skew is most pronounced among eusocial species, in which one or a few group members do all the reproducing while most are obligately sterile workers. In these cases, the whole group may be one big family, and high levels of altruism are common. Group endogamy, too, will increase within-group relatedness. Hamilton (1975:142–43) argues that endogamy can make kin selection relevant even in fairly large groups. In the island model of population structure originally developed by Wright, in which a population is divided into a number of demes of population n and rate of immigration m , the within-group coefficient of relatedness will tend over the long run to an equilibrium value of $r \approx 1/(2nm + 1)$ (assuming $m \ll 1$). Because this value depends only on the absolute number of immigrants (nm), Hamilton argues that even large groups can have coefficients of relatedness between their members comparable to those within families, provided that they are strongly endogamous.

In our species neither reproductive skew nor group endogamy is likely to be strong enough to make individual nepotism very important in large groups. Reproductive skew may be moderately important among men in some populations, owing to polygyny, but women’s potential rate of reproduction is far too low to allow the extreme female reproductive skew seen in some other species. And while endogamy by definition increases coefficients of relatedness within groups, these coefficients will nevertheless decline with increasing group size as long as large groups have greater absolute numbers of immigrants per generation than small groups. Levels of immigration in large kin groups are unlikely to be low enough (a few individuals per generation) for long enough (tens or hundreds of generations) to turn each such group, in effect, into one big family.

Do large kin groups present any better prospects for group nepotism? Jorde (1980) reviews data on genetic structure in a number of human populations. Table 1 presents data from the tribal societies in his sample. I have calculated average coefficients of relatedness (r_{11}) and group coefficients of relatedness (r_g) based on figures Jorde gives for coefficients of inbreeding (Wright’s F_{ST}) and sizes of population subdivisions. Group coefficients of relatedness are calculated based on equation 2, assuming

TABLE 1
Coefficients of Inbreeding (F_{ST}) and Individual and Group Coefficients of Relatedness (r_{11} and r_g) in a Sample of Tribal Societies (from Jorde 1980)

Population	F_{ST}	r_{11}	Number of Subdivisions	Population Size	Subdivision Size	r_g
Papago	.028	.054	10	5,102	510	.936
Juang ("advanced")	.032	.063	5	819	164	.846
Juang ("primitive")	.003	.006	16	1,570	98	.231
E. Highlands of New Guinea	.038	.074	43	122,022	2,838	.991
Fore	.020	.039	19	13,529	712	.936
!Kung	.007	.013	6	2,200	367	.712
Yanomami	.063	.119	37	1,200	32	.687
Makritare	.036	.069	7	2,000	286	.914
Xavante	.007	.013	3	1,750	583	.797
Australian tribes	.040	.077	10	500	50	.676
Median	.030	.058	10	1,875	326	.822

that half the members of a population subdivision choose collectively whether to help the other half ($r_{11} = r_{12}$). Where more than one method was used to calculate coefficients of inbreeding, I have taken the median. Where coefficients were given for different time periods, I have used the earliest. For several reasons the figures in table 1 need to be interpreted cautiously. The data do not represent a random sample of tribal societies, although they probably give some idea of the range of variation. Not all researchers involved here corrected figures for sample size, which may lead to overestimates of coefficients of inbreeding. And coefficients of inbreeding are also sensitive to the number and nature of population subdivisions.

With these caveats in mind, r_g values in the table suggest that population subdivisions in small-scale societies very commonly have sizes and average coefficients of relatedness such that high levels of group nepotism are adaptive. In fact, for many groups, $n_1 r_{11} \gg 1$, and r_g is close to 1, so that donor segments should be prepared as far as feasible to impose something like a "Golden Rule" on themselves, assisting recipients as long as recipients' collective gains significantly exceed donors' collective costs. The r_{11} values in the table provide an estimate of the strength of selection for group nepotistic genes: coefficients of selection for these genes are given by $(B - C/r_g)D$, where $D \approx r_{12}(n_1 + n_2)/2n_1$. If, for example, group nepotism imposes a decrease in fitness of $0.1r_g$ on donors for a gain of 0.3 for recipients, then genes favoring group nepotism will enjoy a selective advantage of $0.2D$. To put this number in perspective, a selective coefficient of .01 will carry a gene from 1% to 99% frequency in 11,500 years and a selective coefficient of .001 will carry a gene from 1% to 99% frequency in 115,000 years. The r_{11} values in table 1 suggest that natural selection can cause major changes in the frequencies of genes for group nepotism as long as long periods of time are available (tens of thousands of years) and net benefits are substantial.

In presenting these data, I have assumed that coeffi-

cients of relatedness at loci influencing group nepotism merely track shared ancestry. But in long-lasting groups, relatedness at such loci may also be influenced by selection. Groups politically dominated by supporters of group nepotism may gradually accumulate extra group nepotism genes as a result of within-group selection against opponents; this can be the case even in very large groups with very low coefficients of relatedness over the genome as a whole. Thus in enduring groups which maintain particular social norms over long periods of time, the threshold for group nepotism may be lower and the strength of selection for group nepotism considerably greater than suggested by the figures in table 1.

KINSHIP AND SOCIALLY IMPOSED ALTRUISM

A number of anthropologists have suggested that a distinctive feature of the kinship domain is an ethic of unidirectional altruism: in kin relations, in contrast to other social relations, individuals are expected to behave altruistically toward others simply because they are kin and not from considerations of recipients' power to reciprocate or coerce. Fortes (1969:237-38) writes of "the axiom of amity":

Though the structural connotation which the notion of kinship carries varies widely, the central value premise associated with it is uniform. Kinship predicates the axiom of amity, the prescriptive altruism exhibited in the ethic of generosity. . . . What the rule posits is that "kinsfolk" have irresistible claims on one another's support and consideration in contradistinction to "non-kinsmen," simply by reason of the fact that they are kin. Kinsfolk must ideally share—hence the frequent invocation of brotherhood as the model of generalized kinship; and they must, ideally, do so without putting a price on what they give. . . . Kinsmen must have concern for one another and therefore refrain from wantonly injuring

one another or heedlessly infringing one another's rights. And above all, one may not kill an innocent kinsman as one may a complete alien. It need hardly be added that no society, anywhere, expects these general and diffuse moral prescriptions to be invariably adhered to.

Fortes also notes the wide scope of the axiom of amity: "To the observer in the field . . . the most convincing evidence is not the conduct and sentiments displayed among close kin, but rather the acknowledgement of kinship amity in what seem to be situations where kinship is so tenuous as to be only nominal, as when persons seek out remote clansfolk or classificatory cognates and without further ado claim and receive hospitality and protection" (p. 239). Other anthropologists have recognized the axiom of amity toward kin under a variety of labels: the principle of generosity (Hiatt 1965), generalized—as opposed to balanced—reciprocity (Sahlins 1965), and the ethic of sharing—as opposed to exchange (Price 1975; Lederman 1986:35–37; LiPuma 1988:36).

Fiske (1991), drawing on a large body of evidence from anthropology, social psychology, and sociology, proposes that there are four universal bases of social order, found in one form or another in every human society: communal sharing, authority ranking, equality matching, and market pricing. These four principles constitute a kind of innate grammar of morality, present in all non-sociopathic adults, that different cultures will draw on in different ways in constructing moral codes. The principle of communal sharing (p. 14) corresponds closely to Fortes's axiom of amity:

The important features of Communal Sharing are captured in three English words with a common root: "kind," "kindness," and "kin." . . . All three words are derived from the same Indo-European root, "gin Ω "—meaning to give birth or beget—from which are derived a family of closely linked words: genus, gender, generous, generate, genitor, gentle, genuine, congenital, nation, native, nature, and innate. . . . This family of words captures the essence of Communal Sharing: it is a relationship based on duties and sentiments generating kindness and generosity among people conceived to be of the same kind, especially kin. Participants think of it as a natural, genuine, and spontaneous form of relationship between people who descend from common genealogical roots and thus share a common nature, an "innate" common substance (e.g. "blood").

Thus anthropologists commonly note that kinship systems feature an ethic of altruism, in the sense that individuals are supposed to assist kin in need. However, this altruism is often socially imposed, motivated more by social pressure and a sense of duty than by affection for the recipients. The Merina of Madagascar expect that individuals will assist their kin with the hard work of farming and will not demand any exact return for their

efforts, but this assistance is not exactly voluntary: those who do not meet this expectation are liable to be accused of witchcraft (Bloch 1973:78). Among the Mendi of New Guinea, the strong ethic of within-clan generalized reciprocity, which encourages patri-clan members to assist one another in times of need with no expectation of repayment, depends in part on social pressure: "Some do not participate in clan events because they are simply not interested. Such people are held in low esteem and are sometimes referred to as 'rubbish' men" (Lederman 1986:28). The role of social pressure in kin altruism is especially clear in many matrilineal societies. Among the matrilineal Dobu of Melanesia, "it normally occurs that a great measure of affection springs up between father and child as well as between mother and child." But no matter what a father's personal feelings "there are many things he cannot provide for his children. His village land, his personal name, his skull, his status, his village palms and fruit trees he cannot by any possibility alienate from his sister's child in favor of his own child" (Fortune 1963:15).⁵

These examples illustrate a distinction commonly made by social anthropologists between domestic and jural domains of kinship—between "sentiment" and "structure," in Needham's (1962) memorable antonymy (see also Fortes 1969:60–84; Fiske 1991:21). The domestic domain is the domain of personal attachment; the jural domain is the domain of socially imposed rights and obligations. Relations within the family are generally predominantly domestic but may have a jural component as well insofar as they must conform to social definitions of appropriate behavior toward kin; relations within larger kin groups are predominantly jural. However, the crucial difference between the domestic and the jural is not the size of the groups involved but the different psychological and social bases of behavior. In the jural domain, individuals allocate resources among kin in response not merely to personal feelings about them but to norms backed up by material and symbolic pressures. Rules in the jural domain are not, of course, always obeyed, nor is their legitimacy always uncontested, nor are different rules always consistent with one another.

5. A favorite adaptationist hypothesis for matrilineal inheritance appeals to individual nepotism: a man invests in his sister's children rather than his wife's children when paternity uncertainty is so high that the former are likely to be more closely related than the latter. However, this condition only holds if the probability, ρ , that the average man is the genitor of a child of his wife is less than .27 (Greene 1978, Kurland 1979), which is hard to believe for most matrilineal societies. If inclusive fitness considerations play any role in matrilineality, it is more likely to be through group nepotism. Two brothers acting together will do better genetically to bestow joint resources on their sisters' children rather than their wives' as long as $\rho < .47$ (on the basis of equation 2). Three brothers will do better as long as $\rho < .61$ and four as long as $\rho < .71$. It is unlikely, however, that paternity uncertainty is the whole explanation for matrilineal biases in kinship; variations in women's influence on collective decision making and in the relative enforcement costs of matrilineal and patrilineal solidarity must also be important. (Flinn [1981] emphasizes the role of third parties in matrilineal inheritance; see also Hartung [1985] for a somewhat different argument.)

But considerations of legitimacy, propriety, legality, and morality may nonetheless impose important constraints on individual choice and provide an opening for the operation of group nepotism.

The axiom of amity, operating within a distinct jural domain of kinship, testifies to a widespread human inclination to establish solidary groups which enforce an ethic of generosity toward kin. This principle follows readily from the theory of group nepotism, although it has been repeatedly formulated by social anthropologists independently of the theory. This is not to say that jural kinship involves nothing more than socially imposed altruism. Kinship commonly includes elements of reciprocity as well as altruism; the role of exchange, especially marital exchange, is emphasized by “alliance theories” of kinship (Lévi-Strauss 1969). Much ink has been spilled over the relative importance of the axiom of amity and the principle of reciprocity in specific cases: for example, the extent to which friendly relations between wife givers and wife takers stem from the two sides’ shared descent and the extent to which they stem from reciprocity. But, looking beyond these disputes over particulars, I suggest that *both* the axiom of amity and the principle of reciprocity owe their ubiquity to “fundamental structures of the human mind” (Lévi-Strauss 1969:84). More specifically, I propose that the two principles stem from distinct moral sentiments adapted to solve distinct problems of collective action and that the moral sentiments reflected in the axiom of amity are good candidates for adaptations for group nepotism.

GENEALOGY, RELATEDNESS, AND SOCIAL KINSHIP

Human kin classifications and associated norms of behavior differ between societies and often do not provide a reliable guide to exact genealogical connections. Relatives at different genealogical distances may be lumped together as equally close and equally deserving of assistance, or relatives at equal genealogical distance may be distinguished as differentially related (classificatory kinship). Individuals not genealogically related may be classified as kin (nongenealogical kinship). Classificatory and nongenealogical kinship may be reinforced by folk theories according to which one parental sex makes more of a contribution than the other to a child’s heredity or nonreproductive processes like food sharing or coresidence contribute to relatedness. In Fox’s (1979:142) terminology, “biological r ” (the genetic coefficient of relatedness) may differ from “cultural r ” (the culturally defined closeness or distance of kinship).

Both classificatory kinship and nongenealogical kinship are well documented in the ethnographic literature. They are important because they commonly govern not merely terminology for different types of relatives but the assignment of roles, rights, and duties. In “classificatory” systems, collateral relatives may be assigned to the same kin category as lineal relatives. For example, the kin term for “father” may be applied to father’s brother, often with corresponding implications for other kin classifications: father’s brother’s sons may be clas-

sified as brothers, father’s father’s brothers as grandfathers, and so on. People in societies practicing classificatory kinship usually know who their biological parents are, and they normally distinguish close and distant “fathers” and “brothers” just as Westerners distinguish close and distant cousins. However, they are often ignorant of the exact genealogical connections between themselves and those defined as relatives. If I know that my father’s father and X’s father were “brothers,” I may know what kin term to apply to X and what my rights and duties are vis-à-vis X, but if “brother” is used in a classificatory fashion in my culture I may not know the actual genealogy involved. Thus kin classification can go hand-in-hand with “genealogical amnesia.” And not only may kin of differing degrees be lumped together by classificatory kinship but individuals with no known genealogical connection may be accepted as kin. While kinship normally involves the idea that kin share an underlying natural similarity, nongenealogical kinship may be rationalized by theories in which such similarity is acquired by nonprocreative processes (Strathern 1973, LiPuma 1988). Genealogical connection may be an ideal or prototypical condition of kinship, but it is apparently not everywhere a necessary one (but see Hirschfeld 1986 and comments for a summary of the wide range of opinions on the relation between genealogy and kinship).

In other words, while genealogy is not irrelevant to kinship, individuals often seem to be relatively careless about the exact genealogical connections—if any—that unite them with distant kin. The resulting discrepancies between biological kinship and social kinship are hard to reconcile with the sort of kin recognition mechanisms expected for individual nepotism. They may be more consistent with group nepotism, first, because the assessment of relatedness within and between groups does not require exact knowledge of distant genealogical connections and, second, because group kinship is a function not only of group relatedness but of group solidarity.

First, in assessing average relatedness within and between groups, people may sidestep the problem of exact reckoning of distant genealogical connections by using rules of thumb involving levels of reproductive skew, rates of group endogamy, and other determinants or correlates of within-group relatedness. For example, in a population with high reproductive skew the average individual will have many siblings, so average sibling number may afford information about group relatedness. A rule of thumb directing attention to average sibling number could also play a role in patrilineal and matrilineal biases in recruitment to kin groups. In a polygynous society, the average individual will have more patrilineal than matrilineal siblings (counting half-siblings), and groups tracing descent through the male line will have higher coefficients of group relatedness (Chagnon 1979, Hughes 1988); paternity uncertainty may bias descent in the opposite direction. People may use other rules of thumb to assess group relatedness. Phenotype matching is not very accurate in assessing individual relatedness to distant kin but may prove more reliable in assessing group relatedness as errors cancel out via averaging.

Second, more “sociological” considerations relating to the enforcement of kin group solidarity may also be important in explaining discrepancies between genealogy and social kinship. In the case of individual nepotism the threshold for kin altruism is a function of genealogical closeness (as measured by the coefficient of relatedness). But in the case of group nepotism the strength of altruism depends not only on relatedness but on the ability and willingness of the kin group to enforce a rule of collective nepotism. Given the advantages of pooling nepotistic effort, an individual may behave more altruistically to a relative socially defined as “kinsman entitled to assistance” than to a relative of equal genetic relatedness not so defined. The dependence of group kinship on group solidarity also means that even individuals not genealogically related may be accepted as kin, provided that they take part in group nepotism. The incorporation of nongenealogical kin into kin groups may actually strengthen group nepotism when there are economies of scale in the provision of collective assistance or when nongenealogical kin are especially likely to be donors rather than recipients of nepotism.

In emphasizing the importance of kin group solidarity as a determinant of kinship, the theory of group nepotism fits neatly with a long-standing tradition of social structural explanation in anthropology. Radcliffe-Brown, an early exponent of this tradition, argues that discrepancies between social and biological kinship are not just idiosyncratic cultural variations but instead depend systematically on differences in the strength and form of kin group solidarity. In his discussions of classificatory kinship beginning with “The Mother’s Brother in Southern Africa” he rejects Morgan’s suggestion that the custom is a relic of group marriage and Sapir’s argument that, given such institutions as the sororate and levirate, it may actually track genealogy better than nonclassificatory kinship.⁶ Instead he stresses the importance of social structure, which he understands as a structure of

socially imposed rights and duties. He argues (1952:64) that classificatory kinship is an expression of norms of internal solidarity and external unity of the sibling group (or other kin groups):

The bond uniting brothers and sisters together into a social group is everywhere regarded as important, but it is more emphasized in some societies than in others. The solidarity of the sibling group is shown in the first instance in the social relations between its members. From this principle there is derived a further principle . . . that of the unity of the sibling group . . . its unity in relation to a person outside it and connected with it by a special relation to one of its members.

I suggest that the Brothers Karamazov game and other models of group nepotism presented above can be interpreted as models of the “solidarity of the sibling group,” in which altruism toward siblings is a function not merely of genealogy but of the level of solidarity of the sibling group or other kin groups. Radcliffe-Brown’s discussion is consistent with this line of argument and introduces the further point that a sufficiently solidary sibling group can insist that any of its members has the same obligation as any other to assist kin outside the group. Classificatory kinship’s insistence that a relative outside the sibling group be treated as equally related to all sibling group members and related customs treating kin as interchangeable may act as devices for pooling nepotism.

Indeed, where group nepotism is concerned there may even be advantages to cultivating ignorance of some kin connections. It is commonly believed that kin selection will produce individuals who distinguish as accurately as feasible between kin with different coefficients of relatedness. Hence failure to distinguish between different degrees of kin and between kin and nonkin is evidence that adaptations for nepotism are ineffective or nonexistent. This is true in the case of individual nepotism: an individual who can accurately distinguish between a sibling and a half-sibling in dispensing kin-based altruism will have an inclusive fitness edge over a less discriminating nepotist. In the case of group nepotism, however, exact discrimination of degrees of relatedness between individuals may be not merely unnecessary but disruptive. Consider the complexities of strategic nepotism among honeybees. If the queen of a hive has mated with multiple males, storing the sperm of each in her spermatheca, some workers in the hive will have the same father and be related as full siblings while others will be related only as half-siblings. Several consequences might be expected: for example, workers caring for the next generation of queens—those who will found new colonies—might neglect half-sibling queens to devote more care to full-sibling queens. In fact, a number of studies show that such discrimination is slight or nonexistent, and it is suspected that some workers systematically obscure cues that others might use to distin-

6. Morgan (1963[1877]), in one of the first systematic treatments of the topic, conjectured that at some stage of prehistory groups of brothers entered into promiscuous marriages with groups of sisters. The offspring of these marriages were treated as the common offspring of the group. The equivalence of siblings in classificatory kinship systems is a relic of this stage. Morgan’s speculations about group marriage are now universally rejected by anthropologists. However, Alexander (1979:183–91) notes that, even if group marriage in a strict sense is unknown in tribal societies, institutions like the levirate and sororate (remarriage to the spouse of a deceased sibling), sororal polygyny, and the tacit acceptance of adultery with the husband’s brother may have some of the same genealogical consequences. In other words, he argues that classificatory terminology may actually track genealogy: cousins are regarded as siblings when there is a good chance that they might actually be half-siblings. This suggestion is unlikely to provide a general explanation for classificatory kinship, however, since it applies only to one version of such terminology (specifically bifurcate merging terminology) and only to a fraction of societies employing such terminology. As Radcliffe-Brown argues in criticizing a similar argument by Sapir, it is far more plausible that classificatory kin terminology and the levirate and sororate are correlated because both are expressions of the solidarity of the sibling group. Thus classificatory kinship is likely to have a sociological rather than a strictly genealogical significance.

guish full- from half-sibling queens. When bees work behind a “veil of ignorance” about their exact relatedness to others in the hive, the productivity of the colony may be greater and collective nepotism more effective (Page, Robinson, and Fondrk 1989, Ratnieks and Reeve 1992).

Genealogical information thus plays a more complicated role in group nepotism than in individual nepotism. Collective actors are never as internally coherent or as sharply bounded as individual organisms, and kin groups commonly have genealogical cleavages operating within them and genealogical ties cutting across them. The potential for group nepotism may be strengthened when these cleavages and connections are obscured by such practices as classificatory kin terminology, politically charged theories of procreation, teknonymy⁷ and related naming customs, and fosterage and adoption.⁸ At the same time, the kin group solidarity made possible by such devices will always be partial and conditional. Not only will individuals commonly attempt to evade the obligations to kin proclaimed in official ideology but they will commonly find themselves torn between the claims of alternative and contradictory norms of kin group organization (Kelly 1977).

The theory of individual nepotism generally takes individual organisms as given and asks how much aid each individual should give kin. But the theory of group nepotism cannot simply take groups as given: groups have to be constructed. If we accept that social structure consists in large part of collective norms and the machinery for enforcing them, then the theory of group nepotism is consistent with the conventional wisdom of social anthropology that the social structural principles expressed in systems of kinship are not mere window dressing but have real (although not exclusive) importance in explaining behavior. “In acting . . . according to ‘culturally defined *r*,’ people are not doing the opposite of acting according to ‘real *r*.’ . . . The propensity to redefine ‘*r*’ . . . is as entrenched in the selection process as the propensity to act according to real *r*. In a very profound sense it is just as real, and part of the same process” (Fox 1979: 142).

7. Teknonymy is the practice of addressing or referring to individuals by the names of their offspring, for example, “Mother of Y.” Geertz and Geertz (1964) show how teknonymy in Bali reinforces village solidarity by fostering “genealogical amnesia”—ignorance of potentially divisive genealogical cleavages.

8. Adoption often reinforces kin-group solidarity by weakening potentially divisive parent-offspring ties, a point repeatedly emphasized by contributors to Carroll’s edited volume on adoption in Eastern Oceania (1970a). For example, among the Nukuoro of Polynesia “the cultural message which all adoption acts communicate to all of the parties concerned is that relatives are interdependent and that the maintenance of this network of interdependency must take priority over the wishes of individuals, even such strong wishes as attach to one’s natural children. Adoption . . . is an especially appropriate vehicle for the expression of cultural norms of kin-group solidarity. . . . The claims of particular parents and particular children on each other must give way in the face of the authority of all elders and the requirement that siblings should cooperate” (Carroll 1970b:152; see also Firth 1936:205–6).

Group Nepotism and the Behavioral Ecology of Demand Sharing

According to a widely held view of human evolution, men in subsistence hunting societies hunt in order to provision their wives and children. However, a number of writers have pointed out that this is at best a partial truth; a large share of the catch is often distributed to people other than the hunters and their immediate families. While food sharing within the family may be understandable as a combination of parental effort and mating effort, the basis for food sharing outside the family is the subject of considerable controversy.

Why do hunters share? The main current hypotheses include *variance reduction*, *tolerated theft*, and *showing off*. The variance-reduction hypothesis starts with the proposition that hunting is a chancy business. The successful hunters who refuse to share today’s surplus may find others unwilling to share with them tomorrow when the fortunes of the hunt run differently. In this view, food sharing is an insurance scheme (Kaplan and Hill 1985). According to the tolerated-theft hypothesis, successful hunters share to avoid harassment from the unsuccessful. Unsuccessful hunters have more to gain from food sharing than successful ones have to lose; they are willing to fight to get a share of meat while those who bring home extra meat are unwilling to fight to keep it (Blurton Jones 1983). Finally, according to the show-off hypothesis successful hunters share in order to enhance their status; enhanced status has nonnutritional rewards, including increased sexual opportunities (Hawkes 1991, 1993).

The hypothesis that food sharing among subsistence hunters is a form of kin altruism has received less support. Members of hunter-gatherer bands are almost always connected by ties of kinship and marriage, but patterns of food sharing outside the nuclear family seem inconsistent with those predicted on the basis of individual nepotism. For example, Kaplan and Hill (1985) demonstrate that Ache of Paraguay do not favor close kin over distant ones in sharing food outside the household. However, the role of kinship in food sharing may need to be reconsidered in light of the theory of group nepotism. As the variance-reduction hypothesis suggests, individuals who participate in food-sharing schemes may gain direct advantages if these schemes even out fluctuations in individual hunting success. But given the existence of a group of hunters who share food for this reason, there may be a further inclusive fitness advantage to the group in insisting that each good hunter share food not only with other good hunters but also with poor hunters who are unlikely ever to reciprocate fully, provided that good and poor hunters are kin. Successful hunters faced with a demand for meat from poor relations must consider that failure to share may have repercussions on their relationships with other group members.

Food sharing in hunter-gatherer societies commonly takes the form of demand sharing—members of the

group or particular categories of kin are entitled to demand portions of some food items from successful hunters (Peterson 1993; Kelly 1995:161–81). It is not clear that sharing balances out in the long run; existing data sets suggest that some individuals consistently give more than they receive and vice versa (Kaplan and Hill 1985, Hawkes 1993). In any case, those who demand a share typically appeal to their need and their kin status or group membership rather than to past or potential reciprocity (Bird-David 1990:191). Nor does sharing seem to be simply a function of the relative physical or political strength of the two parties (Kaplan and Hill 1985). Accounts of demand sharing generally stress that sharing is a social obligation and sometimes explicitly cite collective penalties against the stingy. “Sharing food is an absolute obligation to the Batek [of Malaysia], not something the giver has much discretion over. As one hunter said: ‘If I didn’t take the meat back to camp, everyone would be angry at me’” (Endicott 1988:117). At the same time, while individuals may not refuse a direct request to share, they may resort to secrecy and lying to avoid demands for food (Altman and Peterson 1988:88–89).

Kinship is commonly a factor in demand sharing. In some groups, particular kin, including classificatory kin, have special claims on the hunter’s catch (for the Gunwinngu of Australia, see Altman 1987:137–39; for the Siriono of Bolivia, see Siskind 1973:81–84). In other groups all members of the community have equal claims, but this is commonly understood as a kin obligation (Bird-David 1990:191):

[The Nayaka of South India] view . . . themselves as siblings. While the nuclear family is the primary social unit, all groupings beyond it are referred to as *sonta*, which means something like an aggregate of relatives as close as siblings. The people who live in one’s own hamlet are one’s *sonta*, and in other contexts so are all Nayaka who reside in the locality. . . . Most day-to-day interactions between Nayaka concerning food are indeed, as between siblings, conducted in the idiom of “giving” and “requests to be given.”

Insofar as demand sharing of food among subsistence hunters represents socially imposed altruism toward kin, it is just one instance of the axiom of amity or the principle of communal sharing (Price 1975). There are several reasons that this instance is a particularly important one. First, the data on the acquisition and distribution of food which have been collected in the course of the debate over demand sharing offer an especially promising opportunity for quantitative tests of the theory of group nepotism. Second, demand sharing of food is sufficiently widespread among recent hunting-and-gathering societies that we may reasonably infer that it was widespread among prehistoric hunter-gatherers as well. Indeed, it may have been one factor in the ecological dominance of modern human hunter-gatherers. Thus demand sharing of food may have played an important role in human

evolution and in shaping psychological adaptations for group nepotism; the connections observed in many cultures between commensality and kinship might usefully be investigated in this light.

Group Nepotism, Ethnocentrism, and Ethnonationalism

The term “ethnocentrism” was coined by Sumner (1960[1906]:27–30), who argued that human beings everywhere tend to organize themselves into groups, with group members (the in-group) regarding themselves as virtuous and superior in relation to outsiders (the out-group) and upholding a double standard of morality, one that encourages cooperation and altruism toward the in-group but not toward the out-group. LeVine and Campbell (1972), in a review of the ethnographic literature, find that while the full syndrome of ethnocentrism set out by Sumner may not be a human universal (p. 67), ethnocentrism is nevertheless so widespread as to call for a general explanation.

One likely basis of ethnocentrism is the readiness of human beings to discriminate between in-group and out-group. This has been demonstrated repeatedly by social psychologists in experimental settings: when people are divided into groups on the basis of trivial differences or even no differences, they are inclined to favor in-group members in apportioning resources, even when no effort is made to encourage loyalty to the in-group or hostility to the out-group and even when subjects have no face-to-face interaction with in-group or out-group members. Not only do subjects show favoritism toward the in-group but they seem particularly concerned with relative group standing, trying to maximize the difference between in-group and out-group rewards rather than absolute rewards to the in-group. It seems to be group membership per se that motivates favoritism: merely convincing one subject that another is especially similar to him or her is not enough to motivate significant favoritism unless this similarity is used as a basis for assigning group membership (see Billig 1976:340–41 for a review).

If we accept provisionally that this line of inquiry may provide some insight into a panhuman group psychology, it is still important to know what criteria people will use to sort themselves into groups in more naturalistic settings. Of particular interest in this connection is recent research in cognitive anthropology and developmental psychology suggesting that people spontaneously adopt an “essentialist” stance toward certain kinds of biological and social categorization (Atran 1990, Gelman, Coley, and Gottfried 1994, Keil 1994). Living kinds and (some) social categories are seen as having underlying natures that can persist even in the face of drastic changes in outward appearance. Objects in other semantic domains, for example, artifacts, are far less likely to be regarded as preserving their essential natures through similarly drastic transformations. In the social world,

recent studies suggest that children may “be relying on two reasoning strategies to account for regularities in social life—one rooted in the way people enter into habitual interactions and association, the other more concerned with a person’s intrinsic and corporeal nature” (Hirschfeld 1994:218). Children commonly take the latter, “essentialist” stance toward ethnicity—assuming that ethnic identity is normally conserved over the course of growth from child to adult and over the course of reproduction between parent and child—even before they have a clear understanding of what physical characteristics are supposed to be associated with what ethnic groups or of the biology of reproduction. Some writers argue that essentialism in social categorization is a by-product of biological essentialism: people try to make sense of social categories by analogy with living kinds (Boyer 1993, Keil 1994). However, Hirschfeld (1994, 1996) summarizes recent experimental evidence that living-kind essentialism and social-category essentialism, although related, nevertheless constitute two distinct cognitive domains.

Ethnocentrism, then, may result from the combined effects of several widespread psychological phenomena: an in-group/out-group psychology, a model of the social world as divided into kin groups of various sizes defined by underlying natural commonalities, and a disposition to join fellow kin group members, to the extent feasible, in enforcing an ethic of communal sharing. I suggest that this package of psychological mechanisms has group nepotism as one of its evolutionary functions—although parts of the package likely have other functions as well. Further research, especially in developmental psychology, is needed to establish whether and how innate models and motives influence ethnocentrism; an evolutionary perspective may contribute by encouraging researchers to be explicit about which features of human nature contribute to ethnocentrism and whether those features are adaptations or by-products of adaptation.

Ethnically based nationalism (ethnonationalism) in modern societies may provide something of a test case for the group nepotism theory of ethnocentrism. A piece of conventional wisdom in the social sciences is that suprafamilial kin groups have grown weaker under the pressure of political centralization and bureaucratic and legal rationalization. Among tribal peoples, according to this view, kinship is often central to economic, political, and religious life. In traditional states, kinship loses this all-pervading character but may persist in an attenuated form in clan organization and dynastic politics. Finally, in modern bureaucratic states, kinship is largely inconsequential outside the family. The arguments of this paper suggest a revision in this position. With economic development, the decline of local endogamy, and the growth of the state, kin group solidarity has not withered away but has shifted to the level of larger and more tenuously related kin groups—ethnically based nations (ethnonations). If the ubiquitous kindreds, clans, and lineages of tribal societies are expressions of moral sentiments adapted for group nepotism, then ethnonations may be an expression of the same sentiments under

modern conditions. Anderson (1983), in an influential work on modern nationalism, describes nations as “imagined communities”; the theory of group nepotism suggests instead that ethnonations are *imagined kin groups*.

The view that ethnic groups are held together by members’ feelings of kinship is defended by Max Weber and more recently by van den Berghe (1981), Smith (1991), Horowitz (1985), and Connor (1994). In stressing the relation of nationalism to kinship, these writers emphasize that the crucial point is whether members of ethnic groups think of themselves as related, not whether they really are related. In Weber’s words, ethnicity involves “a subjective belief [in] common descent . . . whether or not an objective blood relationship exists” (Weber 1978: 389). The same point holds for the group-nepotism theory of nationalism—the theory claims that modern ethnonationalism is the product of moral sentiments adapted for group nepotism in earlier environments, not that modern nationalism currently advances group inclusive fitness.

Connor (1994:197) is especially forceful in arguing for the role of kin sentiments in ethnonationalism:

With but very few exceptions, authorities have shied from describing the nation as a kinship group and have usually explicitly denied any kinship basis to it. These denials are customarily supported by data showing that most nations do in fact contain several genetic strains. But . . . it is not *what is* but *what people perceive as is* which influences attitudes and behavior. And a subconscious belief in the group’s separate origin and evolution is an important ingredient of national psychology. In ignoring or denying the sense of kinship that infuses the nation, scholars have been blind to that which has been thoroughly apparent to nationalist leaders. In sharpest contrast with most academic analysts of nationalism, those who have successfully mobilized nations have understood that at the core of ethnopscychology is the sense of shared blood, and they have not hesitated to appeal to it.

Connor goes on to document that political leaders of the most diverse ideological strains, including right-wing and left-wing nationalists, communists, and democrats, have frequently and with considerable success appealed to imagined ethnonational kinship to mobilize popular support.

The importance of imagined kinship in nationalism is obscured by the habit of treating “linguistic nationalism,” “religious nationalism,” “cultural nationalism,” “genealogical nationalism,” and “racial nationalism” (or collective racism) as separate phenomena, bearing at best a loose family resemblance to one another and meriting separate explanations. But the observation that nationalists commonly look to language, religion, culture, and physical appearance as visible *markers* of national identity must be distinguished from the claim that these

clues *define* nationality (Horowitz 1986:52–53; Connor 1994:72–73). In the modern world people may fasten onto such tangible criteria to identify nations, but, I suggest, the common implicit assumption that an ethnonation is constituted by an underlying inherited commonality among its members and the accompanying moral sentiments derive not from experience but from an innate ontology of the social world (see also Hirschfeld 1996).

Apart from its intellectual interest, the present account of ethnocentrism and ethnonationalism raises practical political concerns. It is important to keep in mind that the theory of natural selection is a theory of what organisms are adapted to do, not a theory of what they (morally) ought to do or what they must do. Selection at one level is not guaranteed to have beneficial results at more inclusive levels, and nothing in the group-nepotism theory of nationalism implies that nationalism—or group nepotism in general—necessarily benefits the human race or makes a net contribution to human happiness. Indeed, an evolutionary perspective suggests that we should be as skeptical about the moral claims of “higher” motives as of lower ones; moral sentiments are at best a fallible guide to morality (Alexander 1987, Wright 1994). Neither does the present theory imply that individuals *as individuals* will feel any special affection for fellow ethnics or get along badly with members of other ethnic groups. Instead it implies that the influence of ethnocentrism on individual relations will be mediated by social structure—by group solidarity and intergroup politics—a proposition extensively documented in Horowitz’s (1985) study of ethnic conflict. Suprafamilial kin organization is a ubiquitous feature of life in tribal societies, but it varies enormously in its strength and form; by the same token, the theory of group nepotism suggests that ethnonationalism’s hold on individuals will vary with the strength of enforcement mechanisms and that ethnocentric morality will always have to contend with nonkin-based moralities appealing to alternative moral sentiments, to faith, and to reason.

The social anthropology of kinship, demand sharing among subsistence hunters, and ethnocentrism and ethnonationalism are promising test cases for the theory of group nepotism in part because none of these phenomena has a generally accepted explanation. What many existing hypotheses share is the idea that social relations are governed by the exchange of favors or the exercise of coercion. While the theory of kin selection suggests another basis for social relationships—altruism based on genetic relatedness—this theory has often seemed of doubtful relevance to relationships outside the family. But I suggest that we can only appreciate the full scope of the theory of kin selection when we move beyond treating reciprocity and nepotism as mutually exclusive alternatives and consider the many ways in which reciprocity and coercion can act as amplifiers of nepotism.

Appendix

When individuals interact strategically, inclusive fitness calculations do not always give the right answers. An example shows why: If all we know about Dmitri is that he is Ivan’s brother, then we know that the probability that any given gene is identical by descent in the two is $1/2$. If, however, we know about Alyosha not only that he is Ivan’s brother but also that he is willing to cooperate with Ivan in helping Dmitri, then we may have to revise our estimate of the probability that Ivan and Alyosha are identical by descent at any locus affecting group nepotism: this probability is no longer given by the usual coefficient of relatedness. Exact calculations of the fate of genes for conditional nepotism requires explicit population genetic models of the sort presented below.

THE BROTHERS KARAMAZOV GAME

The sexual haploid case. In the case of sexually reproducing haploids, each brother inherits a single copy of a particular gene from either his mother, with probability $1/2$, or his father, with probability $1/2$. This is simpler than the more familiar diploid case in which each individual inherits one copy of a gene from his mother and one from his father, and the calculations from this case will be useful in analyzing the diploid case.

Consider, then, a haploid population in which there are two alleles, G and H , with frequencies p and q , where $q = 1 - p$. Individuals carrying G are more likely than individuals carrying H to be conditional nepotists. The different mating types, their frequencies, and the expected distribution of offspring genotypes are given in table A1, assuming random mating. These results can be used to calculate expected frequencies of eight possible genotype combinations among sibling trios, as shown in table A2. For example, Ivan, Alyosha, and Dmitri may end up all carrying G either because both of their parents carried G (probability = p^2) or because only one of their parents carried G (probability = $2pq$) and all three happened to inherit from that parent (probability = $(1/2)^3$); thus the frequency of sibling trio $G|G|G$ is $p^2 + 2pq/8$ or $(p + 3p^2)/4$.

Table A2 also gives the number of G and H alleles that a single sibling trio of each type would be expected to contribute to the next generation, partitioned into two

TABLE A1
Mating Types and Offspring Distributions in the Haploid Brothers Karamazov Game

Mating Type	Offspring Distribution	Frequency
G and G	All G	p^2
G and H	$1/2G$ and $1/2H$	$2pq$
H and H	All H	q^2

TABLE A2
Conditional Nepotism in the Haploid Brothers Karamazov Game

Sibship			Frequency	G Alleles in Next Generation		H Alleles in Next Generation	
Ivan	Alyosha	Dmitri		Q_G	$+ R_G$	Q_H	$+ R_H$
<i>G</i>	<i>G</i>	<i>G</i>	$P_1 = p^2 + 2pq(1/2)^3 = (p + 3p^2)/4$	$3k$	$- 2C + 2B$	0	$+ 0$
<i>G</i>	<i>G</i>	<i>H</i>	$P_2 = 2pq(1/2)^3 = (p - p^2)/4$	$2k$	$- 2C$	k	$+ 2B$
<i>G</i>	<i>H</i>	<i>G</i>	$P_3 = 2pq(1/2)^3 = (p - p^2)/4$	$2k$	$+ 0$	k	$+ 0$
<i>G</i>	<i>H</i>	<i>H</i>	$P_4 = 2pq(1/2)^3 = (p - p^2)/4$	k	$+ 0$	$2k$	$+ 0$
<i>H</i>	<i>G</i>	<i>G</i>	$P_5 = 2pq(1/2)^3 = (p - p^2)/4$	$2k$	$+ 0$	k	$+ 0$
<i>H</i>	<i>G</i>	<i>H</i>	$P_6 = 2pq(1/2)^3 = (p - p^2)/4$	k	$+ 0$	$2k$	$+ 0$
<i>H</i>	<i>H</i>	<i>G</i>	$P_7 = 2pq(1/2)^3 = (p - p^2)/4$	k	$+ 0$	$2k$	$+ 0$
<i>H</i>	<i>H</i>	<i>H</i>	$P_8 = q^2 + 2pq(1/2)^3 = (4 - 7p + 3p^2)/4$	0	$+ 0$	$3k$	$+ 0$

components, Q and R . $Q_{G,i}$ and $Q_{H,i}$ are the numbers of G and H alleles that would be produced by a trio of type i in the absence of conditional nepotism, assuming k offspring per individual. $R_{G,i}$ and $R_{H,i}$ are the numbers of alleles added to or subtracted from a trio's reproductive output as a consequence of conditional nepotism. If and only if Ivan and Alyosha are both genotype G , then they agree to cooperate in helping Dmitri: each pays a cost of C in reduced offspring numbers, and Dmitri gains a benefit of B from each so that his total benefit is $2B$. Otherwise R_G and R_H are 0 .

Natural selection favors the fittest allele. Assuming an initial population of N , there are initially pN copies of G in the population. In the next generation the number of G alleles is $P_1(Q_{G,i} + R_{G,i})N$ or $kpN + P_1R_{G,i}N$. Dividing this allele number by the initial allele number gives w_G , the fitness of G , which is $k + P_1R_{G,i}/p$. Similarly w_H , the fitness of H , is $k + P_1R_{H,i}/q$. Solving for $w_G > w_H$ gives $B/C > 1/r_{c1}$, where

$$r_{c1} = (1 + 2p)/(2 + 2p). \tag{A1}$$

The effective coefficient of relatedness in this case is different from that in the case of Hamiltonian nepotism. If Ivan were a Hamiltonian nepotist, he would provide benefit B to Dmitri at cost C to himself whether or not Alyosha incurred cost C to provide an additional benefit B to Dmitri. Changing R_G and R_H in table A1 to fit the case of unconditional nepotism and solving for $w_G > w_H$ gives the familiar Hamiltonian $r = 1/2$. By contrast, r_{c1} from equation A1 increases from $1/2$ to $3/4$ as p increases from 0 to 1 . This means that a single conditional nepotist will not be able to invade a population of Hamiltonian nepotists but also that a population of conditional nepotists will be resistant to invasion by a single Hamiltonian nepotist as long as B/C for conditional nepotism is greater than $4/3$.

The diploid case. Diploid organisms like humans carry two copies of every gene (apart from genes on sex chromosomes). They produce haploid gametes—eggs and sperm—which carry one copy of every gene and unite to

make new diploid organisms. For the diploid case, the frequencies of different haploid mating types given in table A1 can be reinterpreted, according to the Hardy-Weinberg rule, as frequencies of different diploid genotypes. And the frequencies of assorted trios of haploid siblings given in table A2 can be reinterpreted as frequencies of assorted genotype combinations among trios of haploid sperm or eggs produced by a single parent. For example, in the diploid case the frequency, $(p + 3p^2)/4$, of genotype combination $G|G|G$ is the probability that all three of the eggs that gave rise to Ivan, Alyosha, and Dmitri carried allele G . Thus table A2 can be used to find the frequencies of each of the eight possible combinations of alleles that three brothers can inherit from their mother. Of course, the same frequencies apply to gene combinations deriving from the father, and pairs of frequencies can be multiplied to give frequencies of all 64 corresponding combinations of maternal and paternal genetic contributions to the trios. For example, the probability that all three brothers are homozygous for G is the probability of inheriting $G|G|G$ from mother and $G|G|G$ from father, which is $(p + 3p^2)/4 \cdot (p + 3p^2)/4$ or $(p^2 + 6p^3 + 9p^4)/16$. Combining equivalent genotype combinations reduces the number of cases to 27. Twelve of these are listed, along with associated frequencies, in table A3. For the remaining 15 cases, Ivan or Alyosha is homozygous for H , and no conditional nepotism takes place; these are combined in the last row of the table. The table also gives the number of G and H alleles that a single sibling trio of each type would be expected to contribute to the next generation, partitioned into Q and R . Costs and benefits of conditional nepotism are assigned as in the haploid case, with the addition of two parameters, h_1 and h_2 . These parameters would normally lie between 1 and 0 and refer to the degree of dominance of the G allele in heterozygotes.

Following the argument laid out for the haploid case, w_G , the fitness of G , is again $k + P_1R_{G,i}/p$, and w_H , the fitness of H , is $k + P_1R_{H,i}/q$. Solving for $w_G > w_H$ gives $B/C > 1/r_{c2}$, where

$$r_{c2} = \frac{2h_2 + p(1 + 4h_1) + p^2(3 - 12h_2) + p^3(2 - 8h_1 + 8h_2)}{4h_2 + p(2 + 6h_1 - 4h_2) + p^2(4 - 2h_1 - 12h_2) + p^3(2 - 8h_1 + 8h_2)} \tag{A2}$$

The simplest assumption about heterozygotes is that they adopt a conditional nepotist strategy with probability 1/2, so that if Ivan and Alyosha are both heterozygotes the probability that they will agree on conditional nepotism is 1/4. On this assumption $h_1 = 1/2$ and $h_2 = 1/4$, and equation A2 simplifies to

$$r_{c3} = (1 + 6p)/(2 + 8p) \tag{A3}$$

The value of r_{c3} goes from 1/2 to 7/10 as p increases from 0 to 1. On the other hand, modifying R_C and R_H to correspond to unconditional, Hamiltonian nepotism and assuming that heterozygote phenotypes are halfway between homozygote phenotypes again results in $r = 1/2$.

Tit-for-tat conditional nepotism in a diploid repeated prisoner's dilemma game. Suppose that there is some chance that Ivan or Alyosha, after agreeing on conditional nepotism toward Dmitri, will cheat. In this case, the two brothers might be caught in something like a prisoner's dilemma game, in which each is tempted to get the inclusive fitness advantages of the other's altruism without paying any of the cost. Axelrod (1984) provides a classic treatment of the prisoner's dilemma game and the evolution of cooperation. He shows that when two individuals play the game with one another repeatedly, a strategy called tit-for-tat is evolutionarily robust. Tit-for-tat means that an individual plays cooperatively as long as the partner does but punishes any noncooperation by not cooperating on the next round.

Tit-for-tat has trouble getting started in a population in which nobody else cooperates, but once established it does better than noncooperation or a host of other, sneakier strategies.

We can apply this line of argument to the Brothers Karamazov game. Suppose that Ivan and Alyosha repeatedly face opportunities to help Dmitri. More formally, suppose that during one round of play each has the opportunity to help Dmitri, and after each round the probability of playing another round is ω . We are interested in the fate of an allele making tit-for-tat conditional nepotism more likely where the alternative is never to help. If Ivan carries such an allele he will help Dmitri on the first round; on each subsequent round he will copy whatever Alyosha did on the preceding round. If both brothers play tit-for-tat and the game lasts the expected number of rounds, $1/(1-\omega)$, then each pays a total cost $-C$ while Dmitri gets a benefit $2B$. If Ivan alone plays tit-for-tat then on the first round only he alone will pay a cost of $-C(1-\omega)$ while Dmitri gets a benefit of $B(1-\omega)$. The costs and benefits accruing to each sibling for the different combinations of strategies are summarized in table A4.

Playing tit-for-tat conditional nepotism is simply equivalent to being a Hamiltonian nepotist on the first round of play and a conditional nepotist thereafter. The payoff is thus just an average of the payoffs to a Hamiltonian nepotist and a conditional nepotist with the payoffs weighted according to how many rounds are played. Tit-for-tat alleles will have greater fitness as long as $B/C > 1/r_{c4}$, where

$$r_{c4} = (1 - \omega) \cdot 1/2 + \omega(1 + 6p)/(2 + 8p) \tag{A4}$$

TABLE A3
Conditional Nepotism in the Diploid Brothers Karamazov Game

Sibship				G Alleles in Next Generation		H Alleles in Next Generation	
Ivan	Alyosha	Dmitri	Frequency	Q_G	$+R_G$	Q_H	$+R_H$
GG	GG	GG	$P_1 = (p^2 + 6p^3 + 9p^4)/16$	$6k$	$-4C + 4B$	0	$+0$
GG	GG	GH	$P_2 = (2p^2 + 4p^3 - 6p^4)/16$	$5k$	$-4C + 2B$	k	$+2B$
GG	GG	HH	$P_3 = (p^2 - 2p^3 + p^4)/16$	$4k$	$-4C$	$2k$	$+4B$
GG	GH	GG	$P_4 = (2p^2 + 4p^3 - 6p^4)/16$	$5k$	$+h_1(-3C + 4B)$	$1k$	$+h_1(-C)$
GG	GH	GH	$P_5 = (4p^2 - 4p^4)/16$	$4k$	$+h_1(-3C + 2B)$	$2k$	$+h_1(-C + 2B)$
GG	GH	HH	$P_6 = (2p^2 - 4p^3 + 2p^4)/16$	$3k$	$+h_1(-3C)$	$3k$	$+h_1(-C + 4B)$
GH	GG	GG	$P_7 = (2p^2 + 4p^3 - 6p^4)/16$	$5k$	$+h_1(-3C + 4B)$	$1k$	$+h_1(-C)$
GH	GG	GH	$P_8 = (4p^2 - 4p^4)/16$	$4k$	$+h_1(-3C + 2B)$	$2k$	$+h_1(-C + 2B)$
GH	GG	HH	$P_9 = (2p^2 - 4p^3 + 2p^4)/16$	$3k$	$+h_1(-3C)$	$3k$	$+h_1(-C + 4B)$
GH	GH	GG	$P_{10} = (4p^2 - 4p^4)/16$	$4k$	$+h_2(-2C + 4B)$	$2k$	$+h_2(-2C)$
GH	GH	GH	$P_{11} = (8p + 16p^2 - 48p^3 + 24p^4)/16$	$3k$	$+h_2(-2C + 2B)$	$3k$	$+h_2(-2C + 2B)$
GH	GH	HH	$P_{12} = (8p - 20p^2 + 16p^3 - 4p^4)/16$	$2k$	$+h_2(-2C)$	$4k$	$+h_2(-2C + 4B)$
All other genotype combinations			$P_{13} = (16 - 16p - 20p^2 + 24p^3 - 4p^4)/16$	$33k$	$+0$	$57k$	$+0$

This equation simplifies to equation A3 as ω goes to 1 and the number of rounds played goes to infinity.

SOCIALLY IMPOSED NEPOTISM AND GROUP RELATEDNESS

Consider a population subdivided into groups, with each group divided in turn into a donor segment and a recipient segment. Each donor segment numbers n_1 haploid individuals and each recipient segment numbers n_2 haploid individuals. (I will consider the diploid case below.) Members of the donor segment are related to one another and related to members of the recipient segment, so that in each group a fraction of genes is identical by descent. Within each group, the genes identical by descent will all be the same allele, while the remaining genes will be a random assortment of different alleles. In the donor gene pool the fraction of genes identical by descent has an expected value of f_1 ; in the recipient gene pool the fraction of genes identical by descent with those in the donor gene pool has an expected value of f_2 . The expected coefficient of relatedness between two random donors is $f_1^2 = r_{11}$ and between a random donor and a random recipient is $f_1 f_2 = r_{12}$. (In the haploid case, the coefficients of relatedness, r_{11} and r_{12} , are Wright's coefficients of inbreeding. In particular, $r_{11} = F_{ST}$ for the donor segment.) We wish to know the expected fate of an allele increasing the probability of collective altruism on the part of the donor segment of a group toward its recipient segment. Such an allele, if present in a sufficiently large proportion of donor segment members, will lead that segment to levy a contribution from all its members which will be donated to all members of the recipient segment.

Let us begin by calculating probabilities of different allele frequencies and corresponding fitnesses. Assume that allele G , which increases the probability of group nepotism, has a mean frequency of p in a large population of groups, all of size $n_0 = n_1 + n_2$ and all divided into donor (population n_1) and recipient (population n_2) segments. The alternative allele, H , which leaves members of donor segments indifferent to the plight of their recipient kin, has mean frequency $q = 1 - p$. Within each group, some number of genes is identical by descent.

TABLE A4
Conditional Nepotism as a Repeated Prisoner's Dilemma Game: The Payoff Matrix

Play Tit-For-Tat Conditional Nepotism?		Expected Payoff		
Ivan	Alyosha	Ivan	Alyosha	Dmitri
Yes	Yes	$-C$	$-C$	$2B$
Yes	No	$-C(1 - \omega)$	0	$B(1 - \omega)$
No	Yes	0	$-C(1 - \omega)$	$B(1 - \omega)$
No	No	0	0	0

Genes identical by descent are either all G (with probability p) or all H (with probability $1 - p$), while the remaining genes are a random assortment of G s and H s.

For integer i , $0 \leq i \leq n_1$, what fraction of groups will have donor segments with exactly i copies of G ? Because an expected fraction, f_1 , of genes in the donor segment is identical by descent and these genes are either all G or all H , we have to consider two cases. In the first case, the genes identical by descent are all G , and the probability that any given gene will be G is $f_1 + (1 - f_1)p$ or $p + f_1 - pf_1$. In this case, the frequency of donor segments with i copies of G is given by the binomial probability density function:

$$P_{1,i} = \frac{n_1!}{i!(n_1 - i)!} (p + f_1 - pf_1)^i (1 - p - f_1 + pf_1)^{(n_1 - i)}. \quad (A5)$$

In the second case, the genes identical by descent are all H instead of G , and the probability that any given gene will be G is $(1 - f_1)p$ or $p - pf_1$. In this case, the probability that i genes will be G is given by

$$P_{2,i} = \frac{n_1!}{i!(n_1 - i)!} (p - pf_1)^i (1 - p + pf_1)^{(n_1 - i)}. \quad (A6)$$

It is also necessary to compute the production of G and H offspring associated with different numbers of G alleles in the donor segment, assuming as before that the number of offspring per individual in the absence of group nepotism is k . Once again there are two cases: either the genes identical by descent in a group are all G or they are all H . In the first case, in which the genes identical by descent are all G , the number of G offspring produced by a group in which i individuals in the donor segment carry G is equal to

$$V_{G1,i} = i(k - C_{G,i}n_2) + n_2(p + f_2 - pf_2)(k + B_1n_1). \quad (A7)$$

The first term on the righthand side is the number of type- G individuals in the donor segment, i , times the fitness of each type- G donor, $k - C_{G,i}n_2$, where each type- G donor pays a cost, $C_{G,i}$, to each of n_2 recipients. The second term is the expected number of individuals of type G in the recipient segment, $n_2(p + f_2 - pf_2)$, times the fitness of each recipient, $k + B_1n_1$, where each recipient gains a benefit, B_i , from each of n_1 donors.

In the second case, in which the genes identical by descent are all H , the number of G offspring produced by a group in which i individuals in the donor segment carry G is equal to

$$V_{G2,i} = i(k - C_{G,i}n_2) + n_2(p - pf_2)(k + B_1n_1). \quad (A8)$$

We still need to calculate production of H offspring for both cases. In the first case, in which the genes identical by descent are all G , the number of H offspring produced by a group in which i individuals in the donor segment carry G is equal to

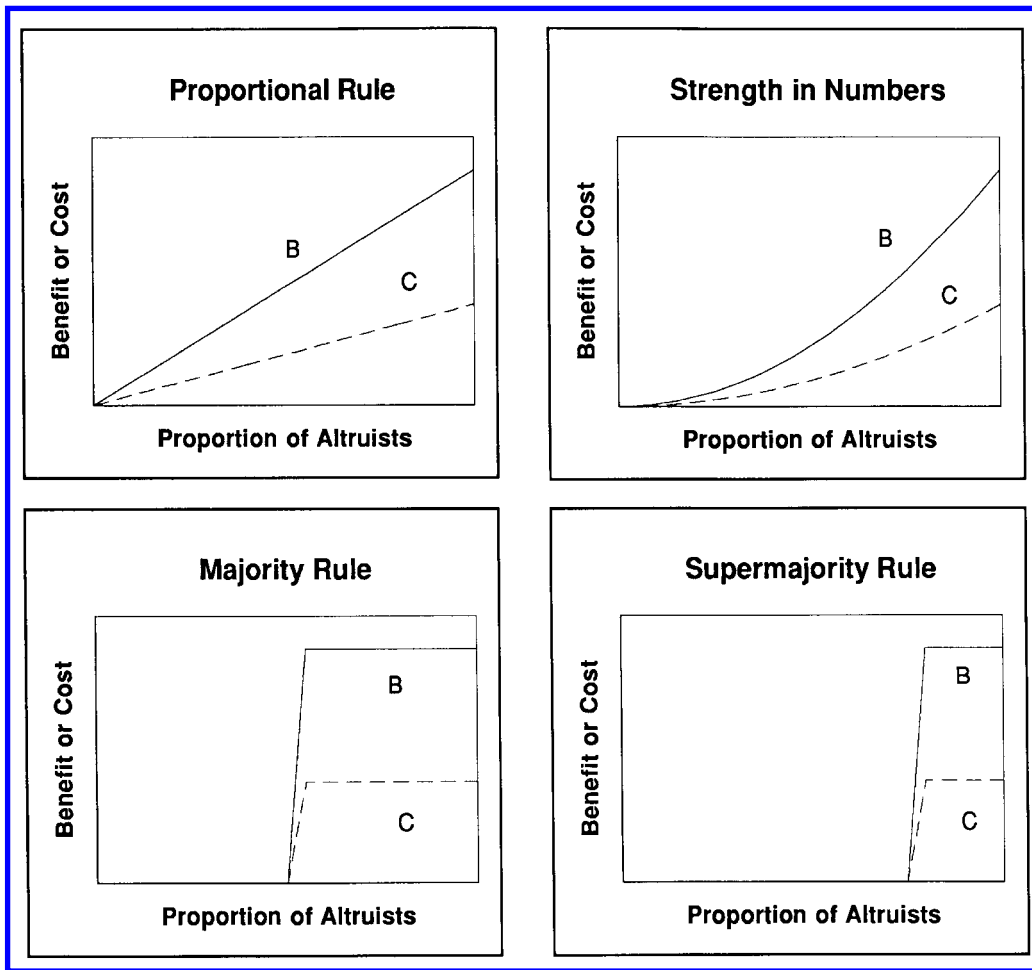


FIG. A1. Variation in the benefits and costs of group nepotism with the proportion of the group in favor under different collective decision rules.

$$V_{H1,i} = (n_1 - i)(k - C_{H,i}n_2) + n_2(1 - p - f_2 + pf_2)(k + B_1n_1). \tag{A9}$$

$$w_H = 1/(n_0q)i=0n_1pP_{1,i}V_{H1,i} + qP_{2,i}V_{H2,i}. \tag{A12}$$

In the second case, in which the genes identical by descent are all *H*, the number of *H* offspring produced by a group in which *i* individuals in the donor segment carry *G* is equal to

$$V_{H2,i} = (n_1 - i)(k - C_{H,i}n_2) + n_2(1 - p + pf_2)(k + B_1n_1). \tag{A10}$$

Summing frequencies and numbers of offspring over *i* for the two cases and dividing by the initial numbers of *G* and *H* gives the populationwide fitnesses:

$$w_G = 1/(n_0p)i=0n_1pP_{1,i}V_{G1,i} + qP_{2,i}V_{G2,i} \tag{A11}$$

and

To find the ratio of benefits to recipient and costs to donor, *B/C*, above which *G* has a higher fitness than *H* ($w_G > w_H$), we must make some further assumptions about how *B_i* and *C_i* change with *i*. In effect, we must assume something about the formal or informal decision rules of donor segments, the rules which determine how much of a contribution a segment will make when *i* of its members are in favor of helping the recipient segment and *n₁ - i* are opposed.

To begin with, assume a system of proportional rule, in which the average level of contribution is directly proportional to the number of individuals in favor and the difference between the contributions of egoists and altruists is proportional to 1 - *S*: then $C_{G,i} = C(Si/n_1 + 1 - S)$, $C_{H,i} = CSi/n_1$, and $B_i = Bi/n_1$, where *B* and *C* are positive constants. Under these assumptions a formula for $w_G - w_H$ can be derived, using the first and second raw moments of the binomial distribution and simplifying:

$$w_G - w_H = \frac{-C(n_1 - Sn_1 + S + Sf_1^2 + Sn_1f_1^2) + Bn_1f_1f_2}{n_1+n_2} \tag{A13}$$

This result can also be written

$$w_G - w_H = \{B - C[(1 - S)/r_{12} + S/r_g]\}D_{hap}, \tag{A14}$$

where

$$r_g = \frac{n_1r_{12}}{1-r_{11}+n_1r_{11}} \tag{A15}$$

and

$$D_{hap} = \frac{n_1r_{12}}{n_1+n_2} \tag{A16}$$

Clearly, with non-zero n_1 and n_2 , the inequality $w_G - w_H > 0$ is satisfied for $B/C > (1-S)/r_{12} + S/r_g$.

The group coefficient of relatedness, r_g , may be derived through another route. The most general definition of the coefficient of relatedness, r , is the regression coefficient of the expected frequency of a gene in the recipient given its frequency in the donor (Wade 1985). For our model, in which donors and recipients are whole groups, this coefficient can be shown to be $r_g' = n_2f_1f_2/$

$(1-f_1^2 + n_1f_1^2)$. In other words, if the frequency of G in the donor segment is $p + j$, then the expected frequency of G in the recipient segment is $p + r_g'j$. This version of the coefficient of relatedness is expressed in terms of the total cost to each donor and the total benefit to each recipient. To derive the r_g given by equation A15, which is expressed in terms of the benefit that a single donor confers on a single recipient, we must multiply r_g' by n_1/n_2 .

The above equations are valid for the haploid case. For the diploid case, if levels of group nepotism depend purely on total numbers of different alleles and not on relative proportions of homozygotes and heterozygotes (that is, heterozygote phenotypes are halfway between the two homozygote phenotypes), then equations A14 through A16 are valid if n_1 and n_2 are replaced by $2n_1$ and $2n_2$, and r_{11} and r_{12} are replaced by f_{11} and f_{12} , where f_{11} and f_{12} are Wright's coefficients of inbreeding. Given that $f_{11} = r_{11}/(2-r_{11})$ and $f_{12} = r_{12}/(2-r_{11})$ for diploids, equation A15 still gives the correct r_g for the diploid case, while the diploid D is approximately $(1/2)D_{hap}$.

Alternative decision rules. Proportional rule, in which the level of contribution is directly proportional to the number of would-be nepotists, is only one possible "voting" scheme. Others include (1) strength in numbers, whereby the ability of supporters of group nepotism to levy a collective contribution from the donor segment varies with the square of the proportion of supporters in

TABLE A5
Effective Coefficients of Relatedness with Alternative Collective Decision Rules

Decision Rule and n_1	p_1	p_2	p_3	p_1	p_2	p_3	p_1	p_2	p_3
$n_1 = 10$									
	$r_{11} = .5$			$r_{11} = .1$			$r_{11} = .02$		
Proportional	.909	.909	.909	.526	.526	.526	.169	.169	.169
Strength-in-numbers	1.04	.909	.904	.571	.526	.511	.186	.169	.164
Majority	1.01	.989	.990	.557	.598	.628	.211	.177	.216
Supermajority	.943	.902	.969	.421	.453	.577	.178	.157	.177
$n_1 = 50$									
	$r_{11} = .1$			$r_{11} = .02$			$r_{11} = .004$		
Proportional	.847	.847	.847	.505	.505	.505	.167	.167	.167
Strength-in-numbers	1.09	.861	.839	.552	.506	.492	.178	.167	.164
Majority	.940	.984	.913	.470	.588	.501	.172	.176	.177
Supermajority	.700	.902	.991	.339	.522	.694	.128	.168	.267
$n_1 = 500$									
	$r_{11} = .01$			$r_{11} = .002$			$r_{11} = .0004$		
Proportional	.835	.835	.835	.501	.501	.501	.167	.167	.167
Strength-in-numbers	.917	.875	.862	.526	.503	.488	.170	.167	.166
Majority	.873	1.003	.870	.438	.587	.449	.157	.176	.159
Supermajority	.552	.874	.987	.260	.508	.637	.106	.167	.227

NOTE: For majority rule and supermajority rule $\{p_1, p_2, p_3\}$ is equal to $\{.36, .5, .64\}$ and $\{.63, .75, .87\}$ with $n_1 = 50$ and $\{.46, .5, .54\}$ and $\{.71, .75, .79\}$ with $n_1 = 500$. Otherwise $\{p_1, p_2, p_3\} = \{.2, .5, .8\}$.

the donor segment, so that the contribution of the donor segment, C_i , is equal to $C(i/n_1)^2$; (2) majority rule, whereby the contribution of the donor segment, C_i , is 0 for $0 \leq i \leq n_1/2$ and C for $n_1/2 < i \leq n_1$; and (3) supermajority rule, whereby the organization of a collective contribution requires support from more than a bare majority. For example, if group nepotism is possible only when supporters outnumber opponents by more than three to one, then $C_i = 0$ for $0 \leq i \leq (3/4)n_1$ and $C_i = C$ for $(3/4)n_1 < i \leq n_1$.

Figure A1 illustrates the different voting rules. Table A5 presents numerical comparisons of the effective coefficient of relatedness (the minimum B/C value for which $w_G - w_H > 0$) for a variety of n_1 , r_{12} , and p values given different rules, assuming B proportional to C where $C > 0$. For proportional rule and strength in numbers, p_1 , p_2 , and p_3 are set equal to .2, .5, and .8. For majority rule and supermajority rule, selection pressures are negligible in large populations when p is far from the critical thresholds of $p_{crit} = 1/2$ or $p_{crit} = 3/4$, so for $n = 50$ and $n = 500$ I have looked instead at selection pressures at the critical p values and two standard deviations above and below them; the relevant p_1 , p_2 , and p_3 values are given in a note.

The numbers in table A5 show that there is some effect of collective decision rules on the effective coefficient of relatedness. Under proportional rule, the effective r is independent of the frequency of group nepotism alleles; under strength-in-numbers effective r decreases with increasing p , so that a gene favoring high levels of group nepotism might be favored at low frequencies but not at high; under majority rule and—even more so—under supermajority rule the reverse is true. Overall, however, differing rules do not result in dramatically different thresholds for group nepotism, so it seems reasonable to use the r_g value given by equation A14 as a rough approximation to the effective coefficient of group relatedness.

Comments

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How is it that human beings tend to act more altruistically towards in-group members than out-group members, even when they are rather distant kin or not kin at all and even when they need not reciprocate the aid provided? Kin selection accounts for altruism only towards close relatives, argues Jones: it is *group nepotism* that explains our amity towards those whose kinship to us is at least as much social and symbolic as genetic. Though group nepotism probably relies on several evolved mechanisms, including the essentials of the ethnic categories children form, the key component stems

from the mathematics of natural selection (and this seems to be Jones's genuinely original contribution): altruism towards even fairly distant kin will be selected for provided (a) that they are group members and (b) that other kin group members also are altruistic towards these mutual if low-coefficient-of-consanguinity kin. How we initially arrived at b is not too clear, but perpetuating such mutual altruism involves both sanctions and solidarity that encourage in-group members to be generous towards one another and to punish any lack of such generosity on the part of their fellows.

Do we need Jones's arguments? The group-level altruism and ethnocentrism he seeks to account for have been explained, for example, by the contributors to Reynolds, Falter and Vine (1987), by Shaw and Wong (1988), by Hamilton (1975, whom he cites but finds inadequate), by van den Berghe (1981), and by me (Barkow 1989: 146–50), among others. Combining Sewall Wright's (1969) "island model" (very briefly discussed by Jones) and the self-predation model of human evolution (which he does not discuss) permits us to go a long way towards accounting for the origins of ethnocentrism and the "axiom of amity." If we assume a population structure of competing (mutual-predation relationship) semi-isolated demes, alleles favoring in-group cooperation would have been likely to increase in frequency in the gene pool. This is because groups *qua* groups with greater internal cooperation and solidarity would have had a competitive advantage over other groups, while, given the presumed environment of frequent intergroup violent aggression, individuals who were good within-group reciprocators and therefore beneficiaries of altruism would have been the most likely to survive and reproduce (see Barkow 1989 for discussion). The interaction of kin selection and reciprocal altruism would also have favored the production of "group altruism" in such demes because the fitness loss to the donor in cases of "cheating" would have been mitigated by the existence of some degree of consanguinity between donor and recipient. Additional possible explanations for group nepotism, focusing on the adaptive advantages of the internalization of social norms, are also to be found in the literature (Hallowell 1960, 1961; Barkow 1976). So, given the wealth of explanations ("conjectures" is the more honest term), do we need additional accounts? Yes, we do.

There are probably weaknesses and counterarguments for all of the above accounts of group altruism/nepotism, but even if there were not, we would find that each one, alone, is at best incomplete. Jones, too, is not giving us the ultimate resolution of the problem of group cooperation and altruism: rather, he is providing a new piece to the puzzle, one which appears to be rather compatible with but distinct from any of the existing pieces. But it is difficult to evaluate the relative importance of each piece, including Jones's. We do know that gene frequencies represent a sort of resultant of forces, a mathematical compromise among a mix of varying selection pressures that may occur at more than one level of selection and are likely to change over time. It seems reasonable to suppose that the psychological mechanisms most likely to

evolve under these conditions are those produced by multiple selection pressures, that is, those that can solve more than one adaptive problem and that also work well with other mechanisms (Barkow 1989). A suite of such mechanisms (some of which Jones seeks to identify) underlies group altruism and ethnocentrism. Under these circumstances, "reverse engineering" to find the one "correct" evolutionary explanation for the origins of group nepotism (or ethnocentrism, altruism, etc.) does not work very well—what we get is a variety of possible and (in this case) mutually compatible scenarios but no easy way to evaluate their relative importance. Still, the piece Jones has here provided does seem to be a substantial one. (And we may be grateful that Jones has deliberately passed by the stale debate over group versus individual selection: see Reeve and Keller 1999 for a discussion of the more productive questions that replace the old debate.)

Parenthetically, there is irony in Jones's espousing, in this supposedly "poststructuralist" age, the argument of the archstructuralist Radcliffe-Brown that much social ritual can be "explained" in terms of its strengthening of social solidarity. It is social solidarity, Jones tells us, that promotes the group's ability to enforce rules for internal altruism without which "group nepotism" would not be adaptive. Perhaps selection for the pleasure human beings take in such rituals reflects the differential survival of demes that, in practicing them, gave themselves the competitive advantage of group nepotism. But if Radcliffe-Brown is to be resurrected, let us note that it is the agenda of his rival, Malinowski, that is here being followed. It was Malinowski (1944) who sought *A Scientific Theory of Culture*, and it is evolutionists like Jones, along with a growing number of other researchers (e.g., Alexander 1979; Fox 1975, 1989; Boyd and Richerson 1985; Boyer 1998; D'Andrade and Strauss 1992; Mithen 1996; Shore 1996; Sperber 1996; Strauss and Quinn 1997; Romney and Moore 1998), who are building one.

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31 III 00

This is a very important paper, since it provides theoretical backbone for a position that has heretofore been held more on faith than on demonstration. In the piece of mine cited (Fox 1979) I argued that the newly minted "individual selectionists" were treating the differences between so-called real genealogical relationships and "culturally defined" genealogical relationships as absolute. Their aim was to provide that only "real" relationships could explain altruistic/nepotistic behavior. I claimed that this was to fall into the very same error as the fiercest of their critics (e.g., Sahlins) in cultural anthropology. It produced an unbridgeable gulf between the two forms of explanation. I thought, in contrast, that logically the two sets of phenomena and hence their ex-

planation were of the same order. To use an even more newly minted metaphor, there were two domain-specific cognitive algorithms, one for individual kin recognition and one for group kin recognition. The logical argument was that once hominids became dependent on culture/language, a selective advantage—in flexibility of adaptation—would go to those that could operate successfully in terms of "culturally redefined r ": those that could categorize kin into groups and act differentially toward different categories so defined. Selection would therefore favor those groups whose members developed this specific cognitive ability—if you like, the ability to operate a classificatory kinship terminology.

I stressed the importance of this for exogamy and assortative mating; Jones rightly stresses "group nepotism"—sharing, reciprocity, collective action, etc. His demonstration of the theoretical advantages that such group nepotism could confer offers striking support for the overall position. At the time, while most sociobiologists accepted some of the technicalities regarding human kinship categories, they felt obliged to dismiss the conclusion on the grounds that it required "group selection," which was self-evidently erroneous. Today we know better, and that early sectarian fervor has given way to a careful analysis of the role of group structure in promoting individual (hence collective) fitness.

There are more things wrong with the adaptationist theory of matrilineal inheritance/descent than Jones allows for. The issue, while relevant, is too complex to go into here in detail, but one major flaw is the argument from low levels of paternity certainty itself. If such certainty were truly low, then for a man the probability of his sister's being a half-sister would be high. If so, then his sister's children would be related to him only in the same degree as first cousins, which in turn would be discounted by half. Such degrees of relatedness would be almost as low as the probability of paternity and would not be enough to trigger investment (see Fox 1993).

On the issue of nationalism and kinship, as he suggests, many observers have noted the use of kinship imagery to rouse patriotic sentiments. But the problem with much current nationalism is that such a device is so implausible that it fails in its purpose. It works with relatively small, homogeneous national—or would-be national—groups (Basques, Kurds, Quebecois). The aim of much nationalistic propaganda, however, has been to unite large, heterogeneous national groups (the United States, the Soviet Union, Canada), where the fiction of common kinship cannot be sustained. Appeals therefore have to be territorial, economic, ideological, or frankly xenophobic rather than nepotistic (see Fox 1997). Given the upsurge of "multiculturalism" stressing ethnic, racial, and linguistic differences, appeals to common kinship are even more difficult to sustain. The only thing that holds a multicultural nation together sentimentally is perhaps the shared value of allowing subgroups to be not even fictively kin to each other without incurring any penalty. The thing that makes for sameness, in other words, is the tolerance of difference.

But these are minor quibbles. Jones's sophisticated

analysis is a fine starting point for further empirical studies to test hypotheses crucial to the theory. Ethnography certainly shows examples that are compatible with the theory, but we need specific hypothesis testing.

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Behavioral ecologists have developed a variety of evolutionary models of cooperation, but all previous models share one unfortunate feature: they work poorly in large social groups. For this reason, the cooperation seen in large human groups has remained enigmatic. In the present article, Jones provides the first model of cooperation that scales in the opposite direction: group nepotism evolves more easily in large groups than in small ones. This is a development of profound importance. Jones's model seems also to solve other problems: the discord between social and genealogical kinship, the role and structure of sharing in small-scale societies, and the phenomenal ease with which humans develop prejudice against outsiders. This model not only sheds light on all of these topics but also relates them all to organic evolution. It provides a unified explanation for what heretofore has appeared as a disparate set of topics. Thus far the empirical applications of the new theory are only suggestive. It will be interesting to see whether strong tests of the theory can be developed.

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This paper offers some interesting new perspectives on familiar questions—the forces favoring cooperation, in-group solidarity, and kinship as a social (rather than a strictly genealogical) construct. If Jones is right, the models of group nepotism he presents could revolutionize our understanding of the forces shaping human sociality. However, I have two major concerns with the approach he takes here. First, the use of population-genetics models to analyze the adaptive significance of group nepotism and collective action creates a gaping chasm between the evolutionary actors—genes for this trait or that—and the complex social behavior and institutions that these analyses are supposed to illuminate. Surely there are causal links from genes to these higher-level entities, but they are so manifold and complicated that the population-genetic formalism makes the arguments less rather than more plausible. Alternative formalisms, such as the evolutionarily-stable-strategy models and optimization models employed in behavioral ecology, adopt the “phenotypic gambit”

(Grafen 1984) of remaining agnostic about the links between replicators and phenotypes and yet have proved remarkably successful in analyzing social behavior in a multitude of species (Krebs and Davies 1997), including our own (Winterhalder and Smith 2000).

My second major concern involves the treatment of collective action—a substantive rather than a methodological matter. Jones rightly stresses the interdependencies that arise from both collective action and genetic kinship. His introduction of conditional strategies into analyses of nepotism does seem to expand the range of phenomena that inclusive-fitness considerations can illuminate. But sometimes the focus on collective benefits shows evidence of thinking bordering on old-fashioned “good-of-the-group” logic. For example, discussing hunter-gatherer food sharing, Jones speaks of “a further inclusive-fitness advantage to the group” from indiscriminate sharing. I'm not sure what this means. Inclusive-fitness effects are measured with respect to individual actors or individual genes, not groups.

Another illustration of this type of problem arises when Jones argues that when group size is greater than two, the “balance of power” favors group members in their struggle to impose norms of cooperation on any one individual. I don't understand his reasoning here, since the n members of a group are individuals with their own somewhat unique interests and (for many social situations) a temptation to shirk their duties both to conform to cooperative norms and to enforce those norms. For any one shirker, there may be $n-1$ others who might punish such shirking, but we must not forget that there are n potential shirkers. Jones suggests that conformity can be imposed “provided the group has the resources to monitor and sanction” its members, but it takes more than resources: since monitoring and sanction are individually costly activities and produce a benefit shared by all group members (whether or not they pay these costs), enforcement of cooperation requires solving an n -person prisoner's dilemma. It is not at all clear to me that these models of group nepotism solve the fundamental problem of collective action.

Ultimately, the usefulness of group-nepotism models will depend on their ability to generate testable hypotheses and on the empirical success of such hypotheses. At this point I don't know what such hypotheses and tests would look like, though I am open to the possibilities. Jones argues that “quantitative tests of the theory of group nepotism” are possible, but this promise remains murky to me. If he and others can move beyond single-gene models and plausibility stories about the evolution of traits controlled by these alleles to richer, more contextualized, and above all testable hypotheses, then this promise might be fulfilled.

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We endorse much of Jones's excellent discussion of how collective action is relevant to understanding kinship. We think it is impossible to understand human sociality, including kinship dynamics, without appreciating the role that selection relating to collective action has played over evolutionary time in building into the human psychological architecture a specialized coalitional psychology with its own distinctive procedures and circuitry (Tooby and Cosmides 1988). The ancestrally stable features of situations involving the intersection of collective action with kinship, coalitional aggression, and production should have selected for a suite of neurocognitive adaptations in the human mind that are computationally organized to perceive, represent, and motivate the solutions to the adaptive problems embedded in these repeated games. Conditions favoring collective action are so commonly impacted by kinship that kin selection must inevitably have shaped significant aspects of coalitional psychology.

As we analyze them, activities involving collective action are cognitively represented and behaviorally regulated primarily as a form of social exchange or reciprocity, and we have found extensive evidence that there are species-typical, neutral distinct cognitive adaptations specialized for reasoning about social exchange, including social laws (Cosmides and Tooby 2000). The intercontingent regulatory structure governing n -person social exchange can be abbreviated as "For individuals 1 through n , I (individual₁) will do x_1 if individual₂ does x_2 and individual₃ does x_3 . . ." (or "I will if you will"). When acts in the set are made contingent on other acts' performance, then individual₁ receives not only benefit b_1 but the sum of the benefits to her or him of all acts undertaken by all of the individuals in the set that would not otherwise have been undertaken without her or his participation (the baseline condition). In the extreme case of complete intercontingency, each individual faces a payoff structure in which one's own participation or nonparticipation makes possible or blocks others' participation and hence makes possible or blocks the harvesting of new benefits possible only through joint action. Some of the components that we propose characterize this suite of cognitive adaptations are:

1. *Adaptations for detecting possible mutual gain.* Collective action would not be possible without the ability to scan the social world, representing, analyzing, and detecting situations that have the potential for accruing gains through coordinated action or mutually followed rules of conduct (norms). Specializations must be able to generate representations of alternative projects or rules of conduct that apply across sets of individuals, as well as compute the effect of alternative rules or courses of action on the actor's own welfare and on how others

will perceive their own welfare. That is, they must be able simultaneously to represent the self as merely one individual parallel to others (decentering) while maintaining a motivational system inclined to promote the best outcome for the self. Therefore, we think humans evolved a "theory of interests" (like "theory of mind")—a conceptual format that represents others' relations to potential and actual situations in terms of an abstract summary of their motivations ("self-interest"). Such cognitive adaptations are one major precondition for the emergence of local cultural systems of morality or justice. In the case of kin-based collective action ("kinship systems"), it is useful to be able to achieve the representation of others' interests in a common format that allows the mutual identification of which coordinated projects or norms will have sufficiently widespread appeal. For this reason, we believe that selection has shaped a species-typical conceptual format involving dimensions and primitives for representing kinship (such as sex, generation, lineality, affinity, and so on) that are likely to be relevant to generating possible rules that a sufficient number of people will recognize as simultaneously self- and mutually beneficial (that is, that allow situations and interactions to be framed in ways that highlight potential interindividual parallels in interest). Another powerful cognitive extension is the ability to represent groups, in part, as "individuals" or agents that can have interests, obligations, intentions, beliefs, statuses, and so on, in much the same way that individuals do.

2. *Defensive specializations against free riding.* Cheater detection circuits are required if n -person social exchange is to evolve and be evolutionarily stable. To function, cheater detection circuitry needs to be coupled to a component that modulates one's own level of compliance in response to others' levels of compliance. Such circuitry motivates greater effort when others are investing sufficiently (and contingently) and lower effort in the presence of free riding or indiscriminate investing. Hence, the presence of free riders threatens and may trigger the dissolution of an otherwise mutually beneficial intercontingent effort. Selection favored, where feasible, circuitry that embodies less costly alternatives to abandoning a potentially beneficial common enterprise. Therefore, our coalitional psychology also has available components motivating exposure of cheaters (or those investing the least) and their punishment or exclusion (such as recategorizing them as non-kin or no longer considering proposals originating from them for joint action, as when exposed hypocrisy undermines the position of someone to enforce a norm). Procedures for social comparison should be motivationally important and involve the representation of *own welfare* and *group welfare* and the comparison of one's own contribution and others' contributions on both an individual-by-individual and a pooled basis. Are others contributing less than I?

3. *Elements designed to promote reaching greater mutual benefit.* Since mutual benefit through collective action is hard to achieve and easy to undermine, collective action levels will often be far lower than optimum. The

recurrent opportunity to capture these unrealized benefits selected for design elements that promote upward movement, including an initial cooperative orientation somewhat parallel to tit-for-tat's opening cooperative move. This orientation involves a readiness to make the first move, initiating new upward movements at the beginning of any new event boundary that plausibly invites new collective projects, coupled to a decision-rule to modulate downwards if the effort goes unmatched. We recognize others' supernormative initiatives (we can be "inspired" by others, a complement to our being cooled by hypocrisy or defection). We are proud of our own supernormative efforts, especially if they successfully induce higher efforts in others, and shamed if our efforts are discovered to be lower than others', inhibiting positive interactions. The motivational system should be more willing to make an investment if it is public. Investments should tend to be made in a continuous flow of consecutive increments (where this is not inconsistent with public delivery), so that their magnitude can be modulated contingent on others' degree of matching—a pattern that reduces the opportunity for free riding. An evolved moral sentiment that generates a negative reaction to reclaiming benefits already delivered to kin acts like a valve that continuously invites efforts upwards through matching: Once a benefit is given, others must match it, or their failure to do so will establish the future collective ceiling below the optimum.

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10 IV 00

Jones's punchline is in fact the last sentence of his article: "But I suggest that we can only appreciate the full scope of the theory of kin selection when we move from treating reciprocity and nepotism as mutually exclusive alternatives to considering the many ways in which reciprocity and coercion can act as amplifiers of nepotism." The first half of the sentence is a throwback to the silly debate between "descent" and "alliance" theorists of the 1950s and 1960s, which, I should hope, has been laid to rest long ago. The second half is a precise summary of a theory of human sociality I explicitly developed some 20 years ago in two books (van den Berghe 1979:14–16; 1981:7–11) devoted respectively to human systems of kinship and marriage and to ethnic relations, two of the three applications presented by Jones.

The question, then, becomes, What does Jones's concept of "group nepotism" add to this triad of sociality mechanisms? Indeed, what is "group nepotism" if not a compound of all three: nepotism, plus reciprocity, plus coercion? Before we invent a hypothetical "group nepotism" distinct from the individual one and underpinned by murky "moral sentiments," the principle of parsimony dictates that we ask whether the mutually reinforcing effects of individual nepotism, reciprocity, and

coercion leave an unexplained residual. I have yet to see even suggestive evidence that they do.

To be sure, people have a capacity to invent and enforce rules that promote the fitness benefits of nepotism, reciprocity, and coercion and that enhance the reciprocal effects of these mechanisms for at least some members of their social group. We call these rules "culture," and they make up the jural structure of human societies. To be sure, we can manipulate, exaggerate, or even invent kinship; we can fake reciprocity, and we can disguise naked, coercive exploitation as benevolence. Our social games and contracts are partially autonomous from the underlying biological calculus of individual fitness maximization and even, occasionally, antithetical to it. Such is the nature of our dual evolutionary trajectory: biological and cultural. However, on parsimony grounds we must invoke group selection, as Jones's "group nepotism" seems to do, only if the three basic individual-level mechanisms leave something unexplained.

Let us take the same three applications of Jones: food (especially meat) sharing, systems of kinship and marriage, and ethnicity. Let us begin with the primordial gathering-hunting hominid group. They practiced nuclear-family inbreeding avoidance through adolescent dispersal, as do countless other social mammals. They hunted cooperatively and shared meat, as do most other social carnivores (e.g., orcas, canids, hyenas, lions). They exchanged mates between neighboring bands, as indeed do other large social mammals. With culture, this primordial group gradually led to much larger and more complex societies. If you keep mating with the boy or girl at the next waterhole, you soon form a breeding population, an *ethny*, bounded by endogamy and made up, over a few generations, of people who cooperate as kin, as mates, and increasingly as both. Group solidarity is, at once, an inextricable mixture of nepotism and reciprocity, with, so far, little coercion beyond age and sex differences.

These social ties, however, become quite weak and diffuse beyond a couple of hundred individuals. What to do if you want to form stronger, larger groups to compete successfully for scarce resources with conspecifics? You invent a system of kinship and marriage based, for instance, on unilineal descent and clan exogamy, as is characteristic of most pastoralist and horticultural societies, which typically number thousands of members. Now you marry outside your lineage and clan but within your ethny.

The lineage or clan becomes a kin group organized for the inheritance of property, the formation of extended households, and various other forms of collective action, and the other lineages and clans become partners in reciprocal ties of marriage, military alliance, and so on. After several generations of clan exogamy, your spouses and in-laws become kinsmen as well, and nepotism and reciprocity continue to be the two sides of the same fitness-maximization coin. If you want to make the system tighter yet, you pass a rule of preferential cross-cousin marriage, so that you now marry the closest kin of your generation outside your clan. At the highest level, the

endogamous group becomes the ethny held together by the warp of nepotism and the weft of reciprocity. As noted by Whitmeyer (1997), fellow ethnics look at each other not only as kin, however distant, but also as potential spouses or in-laws for the nearer family. Every fellow ethnic becomes a potential partner in privileged reciprocity.

Need more cohesion, strength, and numbers? Enter the state, with its exponential increase in coercion, inequality, and exploitation. Now you can form societies running into the millions. If the ties become too loose for comfort, you can invent various fictions, such as that the king is the father of his people or that the state is the political embodiment of the ethny. Hence the power of nationalism.

Where, in all this, do we need “group nepotism” to explain sociality? What we need to understand is how individuals invent and manipulate rules to self-serving ends, that is, consciously or unconsciously play a complex game involving nepotism, reciprocity, and coercion, all laced with a good dose of deceit. To label a policed reciprocity between kin expressing nepotism toward other relatives “group nepotism” is, as far as I can see, yet another attempt to bring in group selection into human sociality. We should not dogmatically reject group selection in human affairs, but we should first make a convincing case for an unexplained residual. Jones, in my view, does not make such a case.

Reply

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It is not news that the study of kinship has been marginalized within cultural anthropology, but even within human sociobiology (behavioral ecology and evolutionary psychology) the study of kinship outside the family has been relatively neglected of late, in comparison with, say, the study of mating strategies and sex differences. I believe that both cultural anthropologists and sociobiologists have neglected the study of kinship in part because it conflicts with their respective origin myths. Cultural anthropology’s origin myth is the story of how a plucky band of cultural anthropologists slew the dragon of reactionary biological determinism in the early 20th century. Like many myths, this one has some truth in it. A lot of early-20th-century innatist theory was poor stuff, and the new cultural determinism incorporated some important advances. But by now cultural anthropology has grown so biophobic that many anthropologists deny any connection between genetic and cultural kinship or even avoid the whole topic of kinship as an embarrassing relic of the past. For sociobiologists the origin myth is the story of how a plucky band of individual selectionists slew the dragon of sloppy good-of-the-species thinking in the 1960s and 1970s. Here again,

there is no question that our understanding of the evolution of social behavior has progressed tremendously over the past 40 years, but it is probably also fair to say that norms and values have been somewhat neglected in human sociobiology. I hope that thinking seriously about both the evolutionary foundations of human behavior and its normative side may revitalize the study of human kinship.

Fox, Rogers, and Smith all note the need for empirical tests of the theory of group nepotism. Behavioral ecology offers one potential avenue for such tests, perhaps as part of a larger project of investigating the role of social pressure and collective rewards and punishments in constraining individual choices in conformity with group norms. Tooby’s work on the psychology of collective action might be relevant here, as might recent theoretical and empirical work on indirect reciprocity (Nowak and Sigmund 1998, Wedekind and Milinski 2000). The cognitive anthropology of kinship may provide another avenue of investigation. For example, Greenberg’s (1966, 1990) pioneering work on linguistic markedness in systems of kin classification suggests that there is a universal psychology of kinship underlying cross-cultural variation in kin terminology and that genealogical distance, relations of dominance and dependence, and norms of kin group solidarity all contribute to perceptions of closeness or distance of social kinship.

Van den Berghe argues that individual nepotism and reciprocity can explain everything for which I invoke group nepotism. He wisely avoids supplying any actual numbers in his argument, and neither here nor in his other publications does he really deal with the fact that, even with some degree of kin group endogamy, individual coefficients of relatedness will normally fall off rapidly outside the family, as shown in table 1. This has made many well-informed evolutionary scholars skeptical about whether the theory of kin selection explains much about sociality and altruism outside the family. Elsewhere van den Berghe (1981) reviews ethnographic and historical evidence to make a strong case for the role of kin selection in tribalism and ethnocentrism, but this hypothesis just doesn’t add up as long as kin altruism is limited to individual nepotism.

Barkow, by contrast, does not deny the likely relevance of group nepotism to human sociality but also stresses that it is only a piece of the puzzle. His brief review of alternative routes to human ultrasociality is a useful supplement to my brief review of models of assortative interaction and cultural group selection.

Smith argues that my discussion of group nepotism contains too little about phenotypes and too much about gene frequencies. I agree to some extent with the first criticism: my rather summary treatment of the mechanics of collective action and the psychology of group behavior deserves to be fleshed out more, perhaps along the lines suggested by Tooby and Cosmides. In extenuation, I can only plead limitations of space, time, and energy. But I strongly disagree that formal population genetic modeling could have been left out of the argument. There are some problems in behavioral ecology

for which optimization models (or the “phenotypic gambit”) are sufficient and explicit population genetic models amount to overkill, but group nepotism is not one of them. Optimization models commonly begin with the proposition that an organism will maximize its inclusive fitness, but this proposition depends on assumptions that are sometimes violated in the present case, in which relatives interact strategically. For example, once I know about Alyosha not only that he is my brother but also that he has chosen a particular strategy, I may no longer be entitled to assume that the probability of our being identical by descent at a locus governing choice of strategy is $1/2$; this is why equations 1 and A1–A3 for conditional nepotism are frequency-dependent and contain a p not found in Hamilton’s Rule. Arguments based on inclusive-fitness maximization can be used retrospectively to explain some of what goes on in models of group nepotism, but my experience is that people hearing these arguments are understandably suspicious and need some reassurance that the formal models work and that group nepotism is not just a scam resting on tricky bookkeeping.¹ For that matter, I wasn’t sure myself that the idea would really work in principle until I had done the math.

Regarding two further points raised by Smith, first, it can be legitimate to measure inclusive fitness benefits and coefficients of relatedness with respect to groups. Thus in equation 2 the group coefficient of relatedness, like the individual coefficient of relatedness, is the regression coefficient of the expected number of copies of the altruist allele among recipients, given the number of copies among donors. I could have rephrased the offending passages in selfish-gene language, but I do not feel obliged always to avoid the language of multilevel selection, which is mathematically equivalent (Sober and Wilson 1998, Reeve 2000). Second, I don’t claim that the present models of group nepotism “solve the fundamental problem of collective action.” Instead, I claim that Boyd and Richerson (1990a, b) among others provide adequate formal models and that people sometimes solve collective action problems in the real world, possibly with the help of dedicated psychological mechanisms (see Boehm 1999 for an excellent recent discussion; also see Edgerton 1985). The question addressed in this paper is thus: “Given a solution or solutions to the problem of collective action, what are the implications for kin selection?”

Regarding two cavils raised by Fox, first, population-wide low confidence of paternity will reduce a man’s expected relatedness not only to his wife’s children but also to his sister and to her children, since she is correspondingly likely to be a half-sister rather than a full sister. This effect, rightly noted by Fox, is already taken into account in Green’s (1978), Kurland’s (1979), and my calculations. Second, many scholars of nationalism con-

trast ethnic nationalism with civic nationalism (Greenfeld 1992, Ignatieff 1994, Connor 1994). If the psychology of group nepotism plays any role in nationalism it is only in ethnic nationalism, with civic nationalism presumably depending instead on the psychology of reciprocity. There is no presumption here that ethnic nationalism or ethnocentrism is always or usually more powerful than civic nationalism.

It is encouraging that this paper has received some very positive responses from a social anthropologist (Fox), a mathematical anthropologist (Rogers), and an evolutionary psychologist (Tooby), along with some more equivocal approval from a behavioral ecologist (Smith). While much theoretical and empirical work remains to be done, I hope that this paper will encourage scholars in a variety of disciplines to consider the interaction of social structure and genetic relatedness in the making of kinship.

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1. Readers who want to get some feeling for the mathematics of the Brothers Karamazov game without wading through the algebra will find it fairly easy to check that equations 1, A1, and A2 give correct results for genotype frequencies corresponding to rare mutants at extreme values $p = 0$ and $p = 1$.

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