
LETNÍ ETOLOGICKÉ ŠKOLY NA FAKULTĚ HUMANITNÍCH STUDIÍ UNIVERZITY KARLOVY

Fakulta humanitních studií UK v průběhu posledních pěti let pořádá letní etologické školy, zaměřené na etologii člověka. Přednášky probíhají vždy v jednotlivých blocích. Každý lektor představuje oblast svého výzkumního zaměření. Studenti mají jedinečnou příležitost poslechnout nejnovější poznatky z oblasti humánní etologie v angličtině a mají také možnost osobního setkání a diskuzi z předními vědci v oboru.

Summary:

*During the past five years, the Faculty of Humanities of the Charles University have held summer ethologic schools focusing on ethology of human beings. The lectures were organized in separate blocks and each lecturer introduced his own area of research. Students thus had an exceptional opportunity to hear in English the latest finding in the area of human ethology and could also meet and discuss personally with leading scientists of this field. During the period we organized these summer schools, our department has been visited (among others) by the following personalities: Prof. Zoya Zorina, Moscow State University, Russia, Dr. Kim Bard, Portsmouth University, U.K., Prof. Ludwig Huber, Vienna University, Austria, Dr. Frank Salter, Laboratory of Human ethology, Max-Plank Institute, Adechs, Germany, Zhanna Reznikova, Dept. of Comparative Psychology of Novosibirsk State University; Laboratory of Community Ethology, Institute for Animal Systematics and Ecology, Siberian Branch RAS, Russia, Dr. Zsofia Viranyi, Dept. of Ethology, Eötvös University, Budapest, Hungary, and Konrad Lorenz Institute for Evolution and Cognition Research, Altenberg, Austria, Dr. Christian Lehmann, Adechs, Germany, Dr. Kirsty Brown, Portsmouth University, U.K. We are presenting two of the lectures that have been presented at our department, during the period these schools were organized and held, in the issue of *Urban People revue*.*

Misunderstandings of Kin Selection and the Delay in Quantifying Ethnic Kinship

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Článek Misunderstanding of kin selection and the delay in quantifying ethnic kinship se zabývala analýzou existujících teorií příbuzenského výběru. Dr. Salter se zabýval velice podrobně pracemi Wiliama Hamiltona o aplikaci teorie příbuzenského výběru na etnický nepotismus vypočtením koeficientu etnického příbuzenství. Další část přednášky tvořilo představení těch vědců a autorit, kteří příbuzenský výběr zavrhli, nebo ho ne zcela dobře pochopili, jako je C. C. Cavalli Sforza, Craig Winter a Richard Lewontin.

Introduction: The quantification of ethnic kinship

When in the mid 1990s I began studying ethnic altruism and conflict from an ethological perspective, I was surprised to find no estimates, however approximate, of the genetic relatedness between co-ethnics. No such estimates were quoted by those who needed them most, theorists who for many years had been studying ethnicity from evolutionary perspectives, especially, Eibl-Eibesfeldt (1979; 1982, pp. 194–5), Grosby (1994), Horowitz (1985), Rushton (1989), Shaw and Wong (1989), and van den Berghe (1978; 1981). The discovery of robust genetic kinship between fellow ethnics would increase the plausibility of these accounts; a low finding would undermine them (Rushton 2005; van den Berghe 2005). Such quantitative knowledge is necessary to apply inclusive fitness theory, the leading biological theory of altruism invented by William Hamilton. When working out his theory, especially his criterion for adaptive altruism, Hamilton took as his starting point knowledge of the coefficient of relatedness between kin of different degrees (hereafter ‘kinship’ will be used in preference to ‘relatedness’). The criterion, now known as Hamilton’s Rule, cannot be applied without knowing these coefficients. Being informed that in

humans full siblings have kinship 0.25 (equivalent to relatedness 0.5), allowed Hamilton to summarize his theory with the memorable sentence:

To put the matter more vividly, an animal acting on this principle would be sacrificing its life adaptively if it could thereby save more than two brothers, but not for less (1996/1963, p. 7).

By an adaptive behaviour, Hamilton meant one that increased or at least preserved the frequency of the actor's genes within the population. The dependence of Hamilton's Rule on knowledge of genetic kinship is general; it applies to altruism between members of any subdivision of a population.

This paper deals with altruism between members of an ethny, by which I mean a named population the members of which believe they descend from common ancestors. Examples include tribes at the smallest scale, modern nations such as the Japanese and the English at the intermediate scale, and autochthonous continental-scale populations, popularly known as races, at the largest scale. If we want to know whether altruism on behalf of fellow ethnics is adaptive for the actor, we must know the kinship or relatedness between the actor and the community he or she is serving. I shall refer to this as the 'ethnic kinship', being the average kinship coefficient between two randomly-chosen members of an ethny. To be altruistic an act needs to risk personal security or personal reproductive fitness. (Although there is disagreement about whether nepotism is a form of altruism, this debate is not material to the present discussion, and I shall be using 'altruism' and 'nepotism' interchangeably. Hence the terms 'ethnic altruism' and 'ethnic nepotism' both mean altruism between fellow ethnics.) Candidates for ethnic altruism include celibate priests, self-sacrificing tribal warriors or modern soldiers, and those who give time, energy, and property to ethnic causes.

Having an estimate of ethnic kinship allows us to calculate the break-even point at which the personal fitness cost of ethnic altruism yields a counterbalancing inclusive fitness benefit to the ethny and hence to the actor. To paraphrase Hamilton, how many fellow ethnics must be saved to make an ethnic nepotist's sacrifice adaptive? Is it one, or ten, or perhaps ten thousand? Quantitative information about ethnic kinship is necessary to apply Hamilton's Rule at the level of populations.

It turns out that ethnic kinship can be surprisingly high, because it is equal to the inter-group variance among populations, based on a derivation by Hen-

ry Harpending (2002), originally argued by Hamilton in an appendix to an early paper (Hamilton 1971, p. 89). Even in competition between closely related ethnics such as the English and Danes, the break-even point for adaptive ethnic nepotism is not very high. Applying Harpending's formulation to the variation data provided by Cavalli-Sforza and colleagues (1994, p. 270; Salter 2002; 2003, Table 3.4), an Englishman would need to save only about 120 fellow ethnics from being replaced by Danish settlers to make his sacrifice adaptive. The break-even point is much lower when the interaction is between different geographical races. For example, an African need save only 2.2 fellow ethnics from being replaced by European settlers to make his sacrifice adaptive (Salter 2003, Table 3.3, derived from Cavalli-Sforza et al. 1994, p. 80).

Ethnic kinship could be significant for theory at one thousandth this level, given the potential importance of small fitness gains in evolutionary processes, and considering that kinship and hence inclusive fitness effects can aggregate, via the mechanism of collective goods, across ever larger populations, from band, to tribe, and nation (Goetze 1998). This finding spectacularly confirms the genetic homology between kin and ethnic group claimed by those who have attempted to extend inclusive fitness theory to population subdivisions beyond the extended family (Eibl-Eibesfeldt 1979, 1982; Hamilton 1971; 1975; Harpending 1979; Rushton 1989; van den Berghe 1978, 1981; E. O. Wilson 1975, p. 573). Knowing ethnic kinship does not constitute a proof. But it does suggest several applications in the study of ethnic conflict and nationalism. For example, quantifying ethnic kinship permits quantification of the fitness effects of an ethny losing territory (Salter 2002). When an ethnic group's relative numbers fall significantly within its territory, every member loses inclusive fitness as assuredly as, and in much greater quantity than, failing to have children (Salter 2002). Little wonder that rapid demographic change is often associated with a rise in identity politics.

The great depth and breadth of ethnic kinship makes it doubly curious that ethnic kinship was not a hot topic during the 1970s and 1980s, when inclusive fitness theory and other neo-Darwinian theories took behavioural biology by storm. There was a clear need to understand ethnicity. Related issues, such as civil wars, nationalism and race relations, have long been factors in domestic and international affairs. While these issues grew in importance after the closing of the Cold War (Huntington 1996), they had contributed to innumerable conflicts, including civil wars and two world wars. Connor (1987/1994, p. 74) points out that from the 1960s instrumentalist theories of ethnicity and na-

tionalism, which viewed ethnicity as a means to other ends such as class conflict, were coming under criticism from scholars who viewed these phenomena as social ties predicated on perceived kinship (Connor 1978; 1987/1994; 1993; Fishman 1985; Horowitz 1985/2000; 1994; Keyes 1976; Kwan and Shibutani 1965; Smith 1981; 1986). Evidence of the extent to which putative kinship corresponded with genetic kinship would surely have greatly bolstered these arguments, or at least have been recognized as significant. Sociobiological theories of ethnic and nationalist altruism were being advanced (especially van den Berghe 1978; 1981), that relied explicitly on Hamilton's theory of inclusive fitness. Shaw and Wong (1989, pp. 221–7) applied a quantitative rational-actor model of fitness maximization in an attempt to explain individual self-sacrifice for family and nation, but without knowledge of ethnic kinship. These perspectives must have been hampered in influencing academic and policy analysis by the lack of information on the scale of ethnic kinship. The research that has been done on ethnic kinship is limited to the evolutionary past, not to contemporary societies (see review in Axelrod et al 2004, p. 1837). Text books in evolution, anthropology, sociology, and politics do not mention the subject. Even evolutionary text books do not provide the up-to-date version of kin selection that opens theoretical space for adaptive ethnic nepotism (Pepper 2000, p. 365; and see next section). Evolutionary research in multi-level selection allows for selection to operate among populations, but has not made use of ethnic kinship based on gene assay data (D. S. Wilson and Sober 1994; D. S. Wilson 2002; but see Harpending 1979). In general, the delay in quantifying ethnic kinship has probably hindered research and the dissemination of knowledge connecting ethnicity to evolutionary theory and population genetics.

The theoretical work needed to estimate ethnic kinship and apply inclusive fitness theory to populations was completed by Hamilton himself in the first half of the 1970s, and by Harpending in 1979. This deepens the puzzle because quantification was within reach, yet no-one bothered to grasp the prize. Why? This paper identifies misinterpretations by leading geneticists and evolutionary theorists that continue to be widely accepted as a basis for rejecting ethnic kinship and related theories. Fallacies and oversights that have impeded the realization of ethnic kinship are described and refuted, usually on the basis of knowledge available in the 1970s and 1980s. Examples are chosen from distinguished scientists who have made large contributions in other areas of genetics, especially L. L. Cavalli-Sforza, C. Venter, R. Lewontin, and R. Dawkins. It is now clear that ethnies do generally have genetic identities, that despite blurred

boundaries they are in fact, not only in myth, descent groups, and that in aggregate, ethnic kinship dwarfs family kinship. First it is necessary to summarize Hamilton's advances towards quantifying ethnic kinship by the mid 1970s.

Contributions by Hamilton and Harpending

Hamilton made three major contributions to extending inclusive fitness theory to ethnic nepotism. First, in his famous 1963 and 1964 papers, he stated his rule for adaptive altruism. In this original formulation, altruism could only be adaptive between individuals whose genes were 'identical by descent'. According to this stipulation, it is insufficient for two individuals to have identical copies of alleles at matching loci. Hamilton thought it also necessary to know how these individuals fit into a known family tree and share a recent ancestor. Holding to this genealogy clause limits inclusive fitness to kin of known descent, so that altruism between anonymous individuals cannot be adaptive, no matter their degree of genetic similarity. According to this formulation, ethnic kinship can only be estimated by tracing extended family trees to establish the average relatedness for the population as a whole. Unfortunately, even where much genealogical data are available, such as in Iceland, genealogies only reach back a limited number of generations, resulting in low estimates of ethnic kinship. In Iceland's case, a highly inbred population with family trees going back ten generations, this method yields an ethnic kinship of only 0.00013 (Gudmundsson et al. 2000), about one thousandth the typical ethnic kinship of 0.125 reported below.

Hamilton's second contribution was to show that inclusive fitness processes can operate beyond the family. In this revision, kinship consists only of identical copies of alleles at the same loci, without any evidence of them being 'identical by descent' (Grafen 1990, p. 46; Pepper 2000). Hamilton explained the change thus, in his 1975 paper:

Because of the way it was first explained, the approach using inclusive fitness has often been identified with 'kin selection' and presented strictly as an alternative to 'group selection' as a way of establishing altruistic social behaviour by natural selection. But ... kinship should be considered just one way of getting positive regression of genotype in the recipient, and that it is this positive regression that is vitally necessary for altruism. Thus the inclusive fitness concept is more general than 'kin selection' (Hamilton 1975, pp. 140-1).

Hamilton's third contribution was to extend inclusive fitness theory to populations, based on the abandonment of the genealogy clause in two papers appearing in 1971 and 1975. In the 1971 paper, 'Selection of Selfish and Altruistic Behaviour in Some Extreme Models', he argued that ethnic kinship is F_{st} , the measure of genetic variance among populations (p. 89), and concluded that altruism between fellow ethnics could be adaptive. There could be 'restraint in the struggle within groups and within local areas in the interests of maintaining strength for the intergroup struggle' (p. 79). In the 1975 paper, 'Innate Social Aptitudes of Man: An Approach from Evolutionary Genetics', he showed that ethnic kinship could, in principle, be high, even with a steady trickle of migration. Near the start of that paper Hamilton stated his hunch about ethnicity and race. '[S]ome things which are often treated as purely cultural in man—say racial discrimination—have deep roots in our animal past and thus are quite likely to rest on direct genetic foundations' (1975, p. 134).

Harpending (1979) came to the same result as Hamilton (1971), concluding that the kinship coefficient between random pairs in a large population subdivision is equal to F_{st} . Like Hamilton, Harpending concluded that ethnic nepotism can be adaptive: 'This will mean that helping behavior within the subdivision will be selected against locally, because kinship is negative locally, but it may be positively selected within the species because kinship between donor and recipient is positive with reference to the global base population' (1979, p. 624).

Thus by 1971, and certainly by 1979, there was a body of theory linking inter-population genetic variance with ethnic kinship and inclusive fitness theory. Further theoretical work has been done along these lines since the 1970s, though with no consensus emerging about whether ethnic altruism was in fact adaptive in the human evolutionary past (Axelrod et al. 2004, p. 1837). This makes it all the more puzzling that it took until 2002, a generation after Hamilton and Harpending published their papers, for the dots to be joined, for ethnic kinship to be quantified, and the break-even point for adaptive ethnic nepotism to be specified (Harpending 2002; Salter 2002). Below I consider likely contributing causes of this delay—disciplinary boundaries resulting in failure to appreciate the significance of ethnic kinship, misleading interpretations of Hamilton's theory, and the academic political culture of the period.

Disciplinary boundaries: Cavalli-Sforza, Venter, Lewontin

The distinguished geneticists N. E. Morton and D. C. Rao (1978, p. 36) noted that disciplinary boundaries were a major cause of disputes and confusions in the study of quantitative genetics, around the time that Hamilton and Harpending published on ethnic kinship. '[E]xternal circumstances have combined to generate vigorous and sometimes acrimonious dispute between disciplines at the limit of mutual comprehension...'

The writings of Luigi Luca Cavalli-Sforza, the leading Stanford geneticist who pioneered the mapping of human genetic variation around the world, illustrate how disciplinary boundaries hindered the quantification of ethnic kinship. The problem seems to have been a lack of appreciation of the significance of that quantity. Like many population geneticists, Cavalli wrote as if unaware of Hamilton's work, even though he co-authored a derivation of Hamilton's Rule for adaptive altruism (Cavalli-Sforza and Feldman 1978). Hamilton's theory took until the mid 1970s to become widely known among evolutionary biologists (Segerstråle 2000, p. 54), when E. O. Wilson (1975) and Richard Dawkins (1976) publicized it in best-selling texts. However, the question remains as to why Cavalli did not explore the theoretical potential of inclusive fitness theory applied to whole populations after the 1970s. In a text co-authored with Walter Bodmer, Cavalli (1976, p. 554) briefly refers to kin selection theory without offering accepted terminology or references. But the culmination of Cavalli's global project, written with Paolo Menozzi and Alberto Piazza, *The History and Geography of Human Genes* (1994), cites no sociobiological theory or theorists. Based on his best known publications, one would never guess that parents had a genetic interest in their children, let alone in their ethnies. The majority of Cavalli's research dealt with matters not impinging on altruism, such as the history of human migration. Yet he also discussed social issues, including those contingent on ethnicity and race, from a Darwinian perspective (1991; 1995; 2000). He denied the genetic reality of these categories, and did not discuss the possible adaptiveness of ethnocentrism.

But, as described above, by 1971 Hamilton had begun to extend inclusive fitness theory to encompass whole populations, and had done so in terms of the variance coefficient, F_{st} , the same coefficient favoured by Cavalli and co-workers. This surely would have been recognized as significant by population geneticists if disciplinary boundaries had not hindered the reception of Hamil-

ton's work. At a minimum it might have been received as a challenge to existing theories of social behaviour related to ethnicity, one deserving of acknowledgement and discussion.

Cavalli was not the only geneticist of note who apparently was unaware of the applicability of inclusive fitness theory at the level of populations. This seems to have been a problem common to big-budget research projects and elite institutions. One high profile example came in June 2000, during U.S. president Bill Clinton's announcement of the first sequencing of the human genome. With him at the podium was J. Craig Venter, the president of Celera Corporation, whose high-speed sequencers had played a major part in the project. Thirty six years after Hamilton's paper on inclusive fitness, and 29 years after the theory was extended to populations, Venter used raw genetic assay data to assert that '[t]he concept of race has no genetic or scientific basis'. The argument became a media mantra: any two humans share about 99.9 percent of their genes, so any genetic differences, including group differences, must be of marginal social importance. Venter did not discuss nepotism, but his sweeping rejection of any genetic basis to race ruled out the adaptiveness of ethnically delimited solidarity. Journalists familiar with the writings of Richard Dawkins (1979, pp. 190-92) could have pointed out that Venter's argument was mistaken if it implied the adaptiveness of universal altruism. Moreover, since Venter's argument was predicated on the assertion of universal human genetic similarity, it implied that parents have no particular genetic stake in their children, a problem also not mentioned by commentators.

Slightly less atheoretical was Richard Lewontin's famous 1972 paper, 'The Apportionment of Human Diversity', which has been endlessly recycled as an argument against the genetic reality of populations, including races. Lewontin is a professor at Harvard University and an important public intellectual contributing to debates touching on genetics and race. Lewontin argued that races (and therefore less genetically distinct populations as well) are too fuzzy to be considered useful categories. Since only 15 percent of human diversity is found among populations, while 85 percent is found among individuals within any one population, the concept of race has 'virtually no genetic or taxonomic significance'. Lewontin also asserted that racial classification has 'no social value and is positively destructive of social and human relations'. The argument has had great influence. For example, in 1998 the American Anthropological Association's executive board declared that 'race is not a direct function of biology, but is rather a creation of society. Human populations are not biologically

distinct groups, and, according to genetic evidence, there is greater variation within racial groups than between them' (AAAS 1998).

Lewontin's argument fails with respect to taxonomy, since individuals can be accurately classified racially both anthropometrically and genetically (Edwards 2003), even when no population possesses unique characteristics. In other words, there need not be sharp qualitative differences to distinguish populations; quantitative characteristics suffice. The statistical method for classifying races has been known since the 1920s, based on the work of Karl Pearson. The method relies on the fact that traits co-vary in lineages, whether families or populations. Combinations of quantitative characteristics such as hair form, skin colour, skeletal proportions, and so on, identify particular populations. Relying on only one trait, such as skin colour, is not always sufficient to distinguish a population. But as more traits are sampled, the reliability of classification approaches 100 percent. Races are fuzzy sets, often indistinct when one trait is singled out for comparison, but crystal clear in overview (Sarich and Miele 2004, p. 209). Applying the same principle to genetic characteristics in a 1963 paper, Cavalli-Sforza and Edwards demonstrated an analysis using data very similar to Lewontin's that sorted 15 populations into an evolutionary tree (Edwards 2003, p. 799). Thus, 'Lewontin's Fallacy', to use Edwards's term, had been demonstrated with respect to taxonomic significance a decade before it was published.

Lewontin's argument also fails with respect to altruism, an important aspect of social relations. Lewontin's own variation data, when translated into kinship coefficients, mean that random pairs of the typical ethny are as related as uncle and niece or grandparent and grandchild in out-bred populations. Unlike earlier proponents of his argument (Boyd 1950; Huxley et al. 1939/1935, pp. 91-2; Livingston 1962), Lewontin might have availed himself of Hamilton's theory, if necessary, to discover that such close kinship is biologically and socially significant, and that kin selection theory also applies to populations. But Lewontin rejected the theory for being adaptationist, reductionist, and politically conservative, as he did the rest of neo-Darwinian theory (Rose, Lewontin, Kamin 1984).

A geneticist of Lewontin's stature did not need to invoke inclusive fitness theory to see the absurdity of dispensing with populations as biological categories. It would have been enough to draw an analogy with the family. According to his argument, if genetic variation within the family is much greater than that among families, then by analogy with race, we should conclude that the fami-

ly is also an unimportant biological aspect of a person; that inherited family resemblances are limited to surface characteristics; and that family members do not have a genetic interest in each other and in the family as a whole.

In fact, intra-family variation is about three times inter-family variation. Fully half of the variation within a population exists within any randomly chosen individual (Harpending, personal communication [see Appendix]; Pääbo 2003). Should we then conclude about families what Lewontin's concludes about race, that they are of 'no social value and is positively destructive of social and human relations'? (As a matter of social policy, some have believed precisely this). Utopian socialism has an anti-family tradition, based on rejection of the discrimination inherent in parental care as competing with universal sharing. Experiments in abolishing the family have been tried by utopian communes and by the early Bolsheviks in the 1920s [Heller 1988]). If one wants to base policy on theoretically unmediated gene assay data, consistency requires accepting that both race and family are biological realities, or rejecting them both as does Marks (2002, p. 135). Lewontin does not adopt this position, but does discount the heritability of traits within families by rejecting the heritability of individual differences. He is critical of the methods of behavioural genetics as applied to humans (including the study of twins), which he considers to be sloppy, often fraudulent, and tainted by bourgeois values (Rose et al. 1984, pp. 95-118). In one popular essay, Lewontin (1996) criticized the nineteenth century novels of Zola and Dickens, for assuming that personality is inherited from parent to child, apparently rejecting the finding of several studies, including the Minnesota Twin Family Study, that about two thirds of the variance in the big five personality traits are genetic in origin, at least in Western societies (Bouchard 1994).

A predictable objection to drawing parallels between variation within families and races is that 25 percent inter-family variation is more significant than 15 percent inter-racial variation. But to carry through such an objection, one would need a theoretically-grounded criterion for determining when the ratio of inter- to intra-group variation becomes significant. For kinship, the accepted criterion is Hamilton's Rule, which tells us that kinship within both families and races are substantial enough to permit adaptive nepotism.

New versions of Lewontin's argument keep being advanced, despite inclusive fitness theory entering the mainstream by 1980. This approach is understandable when limited to the observation that ethnicity and race do not correlate significantly with a particular characteristic or gene. But to reject

race altogether as a valid biological category, while accepting inclusive fitness theory in other contexts, indicates lack of awareness of the theory's extension to populations by its originator. For example, Serre and Pääbo (2004, p. 1683) agree with Lewontin in discounting the validity of the race concept, partly because 'only' 9.2 percent of total genetic diversity occurs among continents.

Not too much weight should be placed on disciplinary boundaries as a cause of the delay in quantifying ethnic kinship. These boundaries demarcate differences in concepts, terminology, and levels of analysis, with attendant differences in research questions. They also reflect differences in social networks, cleavages frequently widened by competition. None of these is insurmountable, as demonstrated by the early sociobiologists who reached outside their discipline of ethology to borrow theoretical tools developed in population genetics. Also, much knowledge was shared between the two disciplines. For example, both Hamilton in ethology, and Cavalli in population genetics, had adopted the gene-centred approach of R. A. Fisher, a founding figure of neo-Darwinism (e.g. see Cavalli-Sforza 2000, p. 22). Hamilton's definition of relatedness is essentially the same as Cavalli's definition of kinship, and both refer to genetic variation as *Fst*. These two groups of scientists were probably aware of one another's work.

Misunderstandings: Richard Dawkins

With the publication of *The Selfish Gene* in 1976, Richard Dawkins became for many the most influential interpreter of William Hamilton's theory of inclusive fitness, dubbed 'kin selection' by John Maynard Smith. Hamilton referred to Dawkins's writings on the subject as brilliant. Dawkins took a special interest in reporting and clarifying Hamilton's theory, not only in *The Selfish Gene* but in numerous scientific papers, most notably 'Twelve Misunderstandings of Kin Selection' (1979), where errors of theory were corrected with verve and learning. He has been a major Darwinian theorist and populariser for a quarter century, illuminating as much as reflecting thinking on the subject. In 1995 he became the Charles Simonyi Professor of Public Understanding of Science at the University of Oxford. *The Selfish Gene* sold millions of copies, and a later string of books has also received much attention. In 2004 he was voted the most influential public intellectual in Britain by the readers of *Prospect* magazine.

If Dawkins had much influence on social scientists' use of inclusive fitness, then the difficulty or reluctance he had in correctly interpreting Hamilton's work on ethnicity probably contributed to the delay in quantifying ethnic kinship. At the minimum his views can be treated as a reflection of general thinking on the subject.

Dawkins did not fully report Hamilton's (1971; 1975) theoretical analysis of ethnic kinship and altruism. Nor did he report Harpending's (1979) similar formal argument that ethnic nepotism—altruism directed towards fellow ethnics—can be adaptive. When it came to ethnic kinship, Dawkins suspended his interest and expertise in nepotism and wrote as though he were on Cavalli's side of the disciplinary boundary, innocent of the Hamiltonian revolution. He appears not have been very interested in the subject scientifically, while firmly espousing the view that ethnic solidarity cannot be adaptive (1981; 1995).

One pivotal issue was, and is, the precise definition of relatedness (or kinship), since this governs the application of Hamilton's Rule for deciding when altruism is adaptive. Abandoning the 'identical by descent' clause, as Hamilton did by 1971, opens the possibility of ethnic nepotism being adaptive. Because Dawkins occasionally retained that clause, he could argue as late as 1995 that: "Kin selection favors nepotism towards your own immediate close family. It does not favor a generalization of nepotism towards millions of other people who happen to be the same color as you" (Miele 1995, p. 83).

Dawkins's writings do not reflect the development of Hamiltonian theory between 1964 and 1975. In some passages he seems to agree with Hamilton's dispensing with the 'identical by descent' clause. The following comes from a 1978 paper:

Individuals do not, in an all or none sense, either qualify or fail to qualify as kin. They have, quantitatively, a greater or less chance of containing a particular gene . . . [T]he post Hamilton 'individual' . . . is an animal plus 1/2 of each of its children plus 1/2 of each sibling plus 1/4 of each niece and grandchild plus 1/8 of each first cousin plus 1/32 of each second cousin . . . Far from being a tidy, discrete group, it is more like a sort of genetical octopus, a probabilistic amoeboid whose pseudopodia ramify and dissolve away into the common gene pool (Dawkins 1978, p. 67).

Here Dawkins implies that an organism extends to the boundaries of any subdivision of the species that carries a concentration of its genes. Since clans,

ethnies, and races are such repositories, one might conclude that Dawkins's interpretation allows for adaptive nepotism between members of these subdivisions. In *The Selfish Gene* Dawkins countenanced the possibility that racial nepotism is sometimes adaptive, even though the behavioural predisposition to do so evolved to benefit small kin groups:

If conditions changed, for example if a species started living in much larger groups, it could lead to wrong decisions. Conceivably, racial prejudice could be interpreted as an irrational generalization of a kin-selected tendency to identify with individuals physically resembling oneself, and to be nasty to individuals different in appearance (Dawkins 1976, p. 100, emphasis added).

In this context, 'wrong' and 'irrational' mean maladaptive. Since 'could be maladaptive' logically entails 'could be adaptive', Dawkins's point is clear: racial nepotism might be adaptive. He emphasizes this by qualifying the opposite possibility as being merely conceivable, not probable.

Similarly, in his 1979 discussion of Hamilton's 1975 (especially p. 142) paper, Dawkins seemed to concur with Hamilton's redefinition of inclusive fitness theory as dealing with genetic similarity rather than with genes identical by descent (Dawkins 1979, pp. 192-3). Earlier he stated: "They do not have to be close kin" (p. 187). His brief discussion accepted the possibility of adaptive ethnic nepotism, when it is intermediate in intensity between family nepotism and hostility to outsiders. Moreover, he appeared to support Hamilton's extension of his model to racial nepotism (1975, p. 144), where the latter reasoned that semi-isolated, inbred populations would probably develop distinctive phenotypes. In that context, Hamilton was saying that adaptive racial nepotism is theoretically possible. Dawkins agreed thus: "[R]andom town members will be more altruistic towards each other than they are to recent immigrants from other towns, for the latter will be noticeably less closely related to them" (1979, p. 193).

Dawkins subsequently developed an hypothesis similar to Hamilton's concerning phenotypic similarity, that he called the 'armpit effect' (1982, p. 146). The hypothesis is that organisms smell, or otherwise inspect, themselves or close relatives, and then search for potential mates and allies who have the same body odour or other inherited characteristic. If the characteristics indicate broader genetic similarity, altruism between the matched organisms stands a chance of being adaptive.

But these passages by Dawkins are mixed with unreconstructed retentions of the 1964 ‘identical by descent’ clause abandoned by Hamilton by 1971. One example is to be found two pages before the amoeboid quote cited above. Neither Hamilton’s 1971 or 1975 paper is referenced in *The Selfish Gene*, in either its 1976 or 1989 edition. As already noted, from the first edition of *The Selfish Gene* (1976, e.g. p. 108) onwards, Dawkins has occasionally asserted that kin selection can only operate between close kin. The ‘identical by descent’ clause was most explicitly defended in his ‘Twelve Misunderstandings’ paper (1979), where Hamilton’s 1971 and 1975 papers were discussed. Here is Dawkins’s discussion of the fifth misunderstanding, concerning universal altruism, where he clarifies precisely what he means by relatedness.

Hamilton’s own way of qualifying the statement [that parents and offspring share 50% of their genes] is . . . to add the phrase ‘identical by descent’ . . . that is, are descended from the same copy of the gene in their most recent common ancestor. The trouble here is that simple verbal reasoning, including thought experiments of the ‘green beard’ type, suggest that selection will in principle favour genes that help copies of themselves that are identical, not merely copies that are identical by descent (Dawkins 1979, p., 191).

Dawkins seemed unsure that Hamilton had eight years earlier abandoned the ‘by descent’ clause. This was not the case in 1982 when *The Extended Phenotype* appeared (1999/1982, p. 153). Dawkins unambiguously argued that ‘kinship provides just one way in which genes can behave as if they recognized and favoured copies of themselves in other individuals’, before quoting Hamilton’s similar view quoted above (1975, p. 153). But there remains an important difference. In his paper, Hamilton explained the adaptiveness of altruism between genetically similar members of population subdivisions, such as ethnies. Dawkins puts the quote to a different purpose, that of criticizing the concept of the fitness-striving organism as ‘vehicle’ or ‘maximizing entity’, instead emphasizing the underlying agency of selfish genes. Yet a few pages earlier he had been arguing that phenotypic matching (the armpit effect) could be adaptive by guiding altruism towards genetically similar individuals, whether close relatives or not. In the early 1980s much of the data on human assortative mating and similarity detection revealed pronounced ethnic clustering (e.g. Thiessen and Gregg 1980), such that it must have been difficult to discuss this phenomenon without speculating whether in humans there are ethnically-distinct arm-

pits, or other indicators of group kinship. Rushton et al. (1985, p. 81-2) did precisely this when they drew on ideas about kin recognition in attempting to explain ethnically-assortative mating and friendship.

The analyses by Hamilton and Dawkins were perfectly compatible, derived as they were from the same neo-Darwinian theory. The point is that Dawkins did not bring up ethnic kinship where apposite—in a section where he had laid out elements of the relevant theory from Hamilton, in a book devoted to the ‘long reach of the gene’, a year after being confronted by the issue of ethnic kinship (Dawkins 1981). When Dawkins did deal directly with ethnicity (1976, p. 100; 1981; 1995; 2004b), ethnic kinship was omitted or treated in desultory manner.

The only twentieth century example I could find of Dawkins offering argument contradicting Hamilton’s theory of ethnic nepotism is in a letter to *Nature* in 1981. There he argued, somewhat cryptically, that applying kin selection to races commits the ‘fifth misunderstanding of kin selection’ quoted from above. Turning to the paper in question (1979) reveals that this particular misunderstanding was committed by the distinguished anthropologist S. L. Washburn. Presaging Venter’s remarks in 2000, cited earlier, Washburn argued that since all humans share the great majority of their genes, kin selection theory predicts that altruistic will be adaptive no matter who the beneficiary; we should therefore expect the altruistic impulse to be non-discriminatory. Dawkins replied that such universal altruism would be maladaptive due to free riders. Applied to ethnic nepotism, the argument is, presumably, that ethnic or racial nepotism is a type of universal altruism, and hence, in Dawkins’s view, vulnerable to free riders. If true, then individuals with a genetic predisposition to show ethnic nepotism suffer lower fitness compared to more selfish individuals. After a few generations, the genes that cause ethnic nepotism would be selected out of the gene pool. In his 1981 letter, Dawkins did not refer to Hamilton’s 1971 extension to populations of Hamilton’s Rule for adaptive altruism, nor to Harpending’s 1979 rediscovery of the principle, both of which conclude that genes for ethnic nepotism can, in principle, increase in frequency. Dawkins mistook ethnic nepotism for universal altruism, an interpretation confirmed by his summary of that letter in the 1995 interview quoted above (Miele 1995). In fact, altruism directed towards ethnies and races in multi-ethnic societies is particular, not universal. The same can be said of the modern world where genetically distant descent groups are brought into competition due to mass transport and international ethnic networking. It was on the basis of these distances, and the

robust ethnic kinship they imply, that Hamilton extended his Rule for adaptive altruism to populations.

Dawkins's 1979 paper contains another misunderstanding of Hamilton's 1975 paper that is reflected in his 1981 letter. In that paper Hamilton concluded that when inbreeding produces a high level of relatedness, sibling-like altruism should emerge between random town members (p. 143). Dawkins sought to qualify this conclusion by noting that altruism is a relative concept. Random town members will only be more altruistic towards each other compared to their treatment of the phenotypically-distinct immigrants. "If the trickle of migrants between Hamilton's towns were to vanish altogether, his prediction of a high degree of within-town altruism would turn out to be tantamount to Washburn's fallacy (Misunderstanding 5)" (Dawkins 1979, p. 193). Note that this is not much of a qualification with respect to the adaptiveness of ethnic nepotism, since immigration is ubiquitous in the modern world, and ethnic nepotism is most likely to be adaptive in multi-ethnic societies. Moreover, Washburn's fallacy concerns universal altruism. But altruism between town members in Hamilton's model would not be universal even if all immigration stopped, because Hamilton's model went beyond interactions between immigrants and natives to include interactions at group boundaries (1975, p. 144). As in the real world, there can be competition between, as well as within, towns, for example over territory and other resources. Taking these qualifications together, Hamilton's model implies a very broad scope for adaptive ethnic nepotism, namely, within multi-ethnic societies and along ethnic boundaries.

Dawkins has continued not to treat seriously ethnic kinship and its implications for social behaviour. For example, in 2004 he published a chapter-length popular discussion of racial differences, in which he expressed opinions on evolutionary causes, and also discussed the psychology and morality of racial identification and discrimination. He embraced Lewontin's position on race, dissenting only by affirming the genetic reality of races, though mainly in genes coding for surface characteristics such as skin colour and hair form. But generally he agreed with Lewontin that the variation among races is small compared to that among individuals within any population. "[Racial variation] turns out to be a small percentage of the total: between 6 and 15 per cent, depending on how you measure it . . . Geneticists conclude, therefore, that race is not a very important aspect of a person" (Dawkins 2004b). As noted in the section on Cavalli-Sforza above, it is true that many geneticists have reached this conclusion regarding physiology and competencies of various kinds. Ra-

cial kinship is another matter, one not discussed. Hamilton thought that kinship is adaptively important, and that has become the mainstream view among evolutionary biologists. Based on his and Harpending's formulation, 6 percent variation among two populations translates into ethnic kinship roughly equivalent to that between a child and its great grandparent, while 15 percent translates into ethnic kinship greater than that between a child and its grandparent. To claim that this is not an important aspect of a person in all social contexts would require the repudiation of kin selection theory.

What caused Dawkins's ambivalent treatment of ethnic kinship? Apart from lack of interest, perhaps scientific paradigm played a part. The reductive, gene-centred way of thinking was a breakthrough that brought many new insights. Thomas Kuhn would have called it a paradigm, and paradigms are somewhat self-contained worlds. One perspective can blind believers to others. As Dawkins has written: "The concept of selection among subroutines in a subroutine pool blurs some important distinctions while pointing up some important similarities: the weaknesses of this way of thinking are linked to its strengths . . . [O]ne of our main leaps forward occurred when . . . we kicked the habit of worrying about individual reproductive success and switched to an imaginary world where 'digging' competed directly with 'entering'; competed for 'running time' in future nervous systems" (1999/1982, p. 131).

Dawkins's history of writings on the subject is instructive because he has long been a central figure in evolutionary biology and highly influential in disseminating the theory of kin selection. His de-emphasis of groups and populations reflected the research priorities common at the time. But his writing skills amplified and disseminated those priorities to a wide constituency, including students and rising academics. His impact cannot be estimated. But textbooks continue to ignore Hamilton's, Harpending's, and other's findings on ethnic kinship. Pepper (2000, p. 365) observes that as late as the end of the 20th century, textbooks on evolution continued to refer to genealogical relatedness when explaining kin selection, although 'the primary literature is in complete agreement that the more general concept of relatedness as genetic similarity is the correct predictor of evolutionary outcomes'. Notwithstanding his creativity and brilliant pedagogy in many areas, Dawkins's misinterpretations of Hamilton's theory, and his desultory application of that theory to ethnicity and race, probably contributed to the study of ethnic kinship remaining muddled and confused for many years.

Academic political culture

In addition to disciplinary boundaries and misunderstandings, there was a general lack of interest in and often active hostility towards the idea of ethnic kinship among the academic elite.

Undoubtedly politics contributed to the delay in extending inclusive fitness theory to ethnies, though this is a poorly researched issue and so will be treated briefly here. With few exceptions, philosophers and historians of science have not dwelt on the political agendas inspiring different positions in evolutionary theory (e.g. Segerstråle 2000; for analyses of political and ethnic agendas see Greenwald and Schuh 1994; Kamin 1974; Lewontin 1970; MacDonald 1998; Rose et al. 1984). The reluctance to discuss bias is understandable. Misunderstandings of fact and theory can be identified and dissected in a reasonably objective manner. But political bias, since usually unstated, is difficult if not impossible to specify. Nevertheless, any account of the delay in quantifying ethnic kinship would be incomplete that omitted politics as a cause, because human genetics encompasses controversies, such as that over nature and nurture, that are among the most partisan in all of science.

Political cultures have scientific agendas, directing interest towards and away from particular ideas. Hamilton recognized the sensitivity of scientific research to non-scientific factors: "To get serious attention in any field ideas do well to have not just factual support but political and human support as well" (1996, p. 322). Non-scientific values often shape scientific agendas, whether they are morally-based ideological principles or pragmatic matters of advancing commercial, career, or group interest. Ethnic altruism and kinship were not considered important to many scientists in a position to apply Hamilton's theory in that direction. Even Hamilton and Harpending, who developed the necessary theory, did not pursue this theme.

Hostility towards the concept of ethnic altruism must be added to lack of interest as a cause of the concept's delayed development. The left, and often minority ethnic activists, generally suspect findings of innate differences between ethnies or classes because they believe that such findings legitimate inequality and exploitation. Bias is not confined to any political orientation. But since the 1960s the left has been ascendant in expressing its values in academic discourse, including mainstream journals. Ignoring or underplaying ethnic kinship accorded with the political orientation of the Anglo-American academic elite, which led and still leads discourse in evolutionary biology, as well as

those with more robust views such as Lewontin and the late Maynard Smith. Highly individualist thinkers as well as those with a universalist vision of society tend to overlook the reality of solidary groups of various kinds, or treat them as inconvenient or irksome obstacles to the ideal society. Lewontin rejected neo-Darwinian theory outright. Maynard Smith was a leading neo-Darwinian theorist, but admitted that his political values made kin selection less intuitive to him, delaying insights and giving time for Hamilton to make the breakthrough.

Rejection of the ideas of ethnic kinship and nepotism has often gone beyond choice of personal research agenda to intolerance of those who choose to research those ideas. Not long after Hamilton had published his theory of ethnic nepotism, the geneticists Morton and Rao (1978, p. 36) observed ideological misrepresentations of quantitative genetics from both the left and right, but saw the former as most influential, including the Marxist group, *Science for the People*, of which Lewontin was a leading member. This group agitated against sociobiology, including kin selection theory. Morton and Rao quoted T. H. Dobzhansky's defence against leftist critiques of genetics:

[T]here are scientists who would proscribe all research on human genetic diversity . . . This research, they argue, is dangerous because its results can be perverted by racists for nefarious ends. That this danger exists cannot be denied. But is pusillanimous evasion a sensible solution? (1976, quoted by Morton and Rao 1978, p. 37).

Politically-motivated opposition to research bearing on ethnic kinship continued for the remainder of the twentieth century, as summarized by Steven Pinker:

In recent decades, the standard response to claims of genetic differences has been to deny the existence of intelligence, to deny the existence of races and other genetic groupings, and to subject proponents to vilification, censorship, and at times physical intimidation. Aside from its effects on liberal discourse, the response is problematic. Reality is what refuses to go away when you do not believe in it, and progress in neuroscience and genomics has made these politically comforting shibboleths (such as the non-existence of intelligence and the non-existence of race) untenable (Pinker 2006).

Intellectual criticism often extended to personal criticism of individual sociobiologists. Fear of ostracism and defamation has probably contributed to the delay in quantifying ethnic kinship. Scientists who researched genetically-influenced group differences were liable to have their reputations assailed by charges of political extremism. From the late 1960s, individuals who spoke openly about biological differences between populations, especially racially distinct populations, risked sanctions in the forms of censorship, damage to reputation, and reduced career opportunities. Hamilton's 1975 paper was called 'reductionist, racist, and ridiculous' by S. L. Washburn (1976, quoted by Hamilton 1999, p. 317). The offending passage (pp. 149—50) speculated that barbarian invasions introduce altruistic genes into old civilizations. Although Hamilton never retracted the idea, this was the last paper he devoted to ethnic kinship. He subsequently criticized his own indirectness in treating the evolution of discriminatory behavior in his original 1964 paper. The intensity of emotions felt at the time is indicated by the harsh judgement Hamilton imposed on himself for skirting issues of ethnic discrimination in his original 1964 paper: "The way of expressing the matter is also indirect and, probably, was cowardly (i.e. aiming to divert from the main point and to avoid sounding racist)." (1987/2001, p. 348). In recent years, even geneticists working to produce more effective drugs by tailoring them to different races have fallen under suspicion (Henig 2004). Some attacks on those propounding genetic theories have been physical, as experienced by the late H. J. Eysenck, E. O. Wilson, and J. P. Rushton. I am not aware of any assaults in the opposite direction, that is, against academics who reject Darwinian science or behaviour genetic. The intolerance of evolutionary analysis and those who pursued it is bound to have discouraged research into ethnic kinship.

Conclusion

While research on ethnic kinship continued after Hamilton's breakthroughs in the 1970s, its volume and visibility were low. Disciplinary boundaries, misinterpretations of Hamiltonian theory, and "political correctness" among academics, contributed to the discovery of the great depth and breadth ethnic kinship being delayed for a generation, impeding the development of biosocial theories of ethnicity and nationalism. Yet by the 1970s the theory and data were at hand to show that ethnies do generally have genetic identities, that despite blurred boundaries they are in fact, not only in myth, descent groups. The

delay in measuring the extent of ethnic kinship was due to kin selection theory not being in place to interpret the data. Even the role of family kinship in the evolution of nepotism is not at all obvious without an understanding of kin selection theory. The belief that that same theory did not apply to populations seems to have led researchers to overlook the largest scale of fraternity.

Appendix:

The apportionment of variation within and among families *Henry Harpending*

[Henry Harpending's derivation of within-family variation is unpublished as I write. Following is his derivation, received as a personal communication.]

If we choose an allele A at some locus that has frequency p in a randomly mixed population, and if we pick a single gene from this population from this locus, the probability that it is A is just p . The variance of this frequency is just the variance of a single Bernoulli trial, $p(1-p)$ or pq if we let $q=1-p$.

If our population of genes is grouped in certain ways, we can partition this variance into within-group and between-group components. We are doing precisely what Lewontin (1972) and others have done, partitioning diversity (variance) into within- and between-group parts.

First consider diploid individuals in a random mating population. What is the variance of the frequency of A in diploid individuals. Since mating is random, diploids are simply random alleles taken 2 at a time. The variance of the frequency of A in samples of 2 is binomial, $pq/2$. This shows that half the variance is among diploid individuals.

Now consider the variance within an individual. Call the frequency in an individual p_2 . The variance of the frequency of A in a single gene chose from an individual is $p_2(1-p_2)$, and this figure averaged over all individuals is

$$\begin{aligned} & \text{Average}(p_2(1-p_2)) \\ &= \text{Average}(p_2 - p_2^2) \\ &= p - p_2\text{-Var}(p_2) \\ &= pq - pq/2 \\ &= pq/2 \end{aligned}$$

since the average of the square of any random variable is the mean of that

variable squared plus the variance of that variable. This shows that half the variance of a gene frequency is within any individual member of a random mating population. We have partitioned the variance into between and within individual components as 1/2 within and 1/2 between. (Once stated, this result is obvious, but I cannot find an earlier reference to it. Perhaps it was considered too obvious to publish.)

Now consider couples chosen at random, that is with no assortative mating. Each couple has 4 copies of A at the locus. Each couple has a frequency of A: it can be 0, 1/4, 1/2, 3/4, or 1. Call the frequency in a clump p_4 , and ask what is the variance of p_4 ? It is just the variance of a binomial with $n=4$ or $pq/4$. We have established that one-fourth of the variance is among couples.

Now consider the variance within a couple. Pick one gene from a couple. The mean is still p and the variance is p_4q_4 . The average value of $p_4(1-p_4)$ over all couples is the average of $p_4 - p_4^2$ which is $p - p^2 - \text{Var}(p_4)$, or $(p - p^2 - p(1-p)/4) = pq(1-1/4) = (3/4)pq$.

This shows that the variance within couples is 3/4 of the total and among couples 1/4 of the total. Another way of saying that 0.25 of the variance is among couples is that the coefficient of kinship of full sibs, offspring of a single couple, is 0.25.

We could continue with larger and larger sets. For example two random couples from a population contain 7/8 of the total diversity, while 1/8 of the diversity is among couples. This partitioning roughly corresponds to that among human races. What this means, for example, is that if humans were to disappear save a single race that would repopulate the earth, the diversity loss would be the same as the loss if two couples from a random mating population were to reconstitute a population.

Acknowledgements

An earlier version was presented at the Annual meeting of the Human Behavior & Evolution Society, Berlin, 21-25 July, 2004, and at the Biennial Congress of the International Society for Human Ethology, Ghent, Belgium, 27-30 July 2004. I thank colleagues at both meetings for their remarks, and Bill McGrew for his useful comments on the same draft. Henry Harpending provided the derivation of the apportionment of variation within and among families.

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The wisdom by social learning

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V přírodě existují tyto tři zdroje učení: genetická dědičnost, individuální učení a sociální učení. Sociální učení probíhá tak, že se učíme buď od ostatních, s ostatními nebo o ostatních. Jedinci, kteří se učí pomocí ostatních, sledují je, mohou vykazovat následující formy sociálního učení: mohou vykazovat zvýšený zájem objevovat, potom co jsou zaujati sledováním činnosti nějakého modelu (sociální napomáhání); mohou být přitahováni k objektu, s kterým model manipuloval (zvýšená stimulace); mohou se účastnit stejného, pro druh typického chování (jako „nakažení“); mohou se naučit něco o vztahu mezi daným stimulem a posílením odměnou při správné reakci (podmiňování pozorováním); mohou se naučit něco o vlastnostech nebo možném využití podnětu (učení napodobováním); mohou se naučit demonstrovanou činnost (napodobování).

Introduction

Members of many species spend a great part of their time in the company of conspecifics. Animals can assimilate essential information by observing their companions, that is, when, where and what to eat, with whom to mate, whom to fear, and how to spend spare time if there is some. In principle, all information can be picked up from internal resources, by development of inherited program. However, social learning and communication give animals great possibilities to improve adaptability and flexibility of behaviour in conformity with concrete and changeable vital circumstances. In many natural situations boundaries between flexibility and conservatism are rather fuzzy. Social learning can sometimes generate behavioural traditions, and some of these traditions can be paradoxically conservative and thus hardly distinguishable from innate forms of behaviour by displays. If we want to know what part of a whole repertoire falls to the share of social learning, we definitely can not gain this