
Letní etologické školy na Fakultě humanitních studií Univerzity Karlovy

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Summer ethological schools at the Faculty of Humanities of the Charles University

Abstrakt

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. Zsafia 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.

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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.

Misunderstandings of Kin Selection and the Delay in Quantifying Ethnic Kinship

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Článek Misunderstanding of kin selection and the delay in quantificating 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 Henry 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 nationalism, 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 argument, 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 (Seeger 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 Hamilton'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 family 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 *F_{st}*. 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 armpits, 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. Racial 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. Segerström 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

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

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 $p - \text{Var}(p_4)$, or $(p - p_2 - \text{Var}(p_4)) = pq(1-1/4) = (3/4)pq$.

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.

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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 knowledge in the mind's eye; instead, we should conduct developmental studies and carry out special experiments. In modern ethology and comparative psychology studying of social learning is a specific and rapidly developing direction with its own notions, definitions and hypotheses. We will consider different forms of social learning, from relatively simple such as social facilitation, to the most complex such as tutoring and maintaining traditions in animal societies. In general, we will develop a concept of how animals acquire information and skills from other individuals by means of observations on their behaviour.

Different forms of social learning

Social learning is said to occur when the behaviour, or presence, or the products of the behaviour, of one individual influence the learning of another (Caldwell and Whiten, 2002).

One of the most complex manifestations of social learning is imitation. Thorndike (1898) defined imitation as "learning to do an act by seeing it done". Basing on his studies of insightful behaviour of animals, Köhler (1925) suggested that imitation demands elements of consciousness and understanding of that a modelling subject possess similar features with the learner. Imitation occurs when observers learn about responses, actions, or patterns of behaviour as a direct result of conspecific observation (Heyes, 1993). Call and Tomasello (1996) insist that for "true" imitation to occur the observer needs both to recognise the goal of the demonstrator and to realise that reaching this goal is only possible by copying the acts of the demonstrator.

The power of simpler than "true imitation" forms of social learning has been underestimated for a long time. "Social learning" in its recent meaning includes a wide range of categories of different levels of complexity. Several phenomena that were once seen as clearly imitative have since been explained in terms of simpler mechanisms resembling imitation.

Contagious behaviour is exemplified by a rule such as "if others are fleeing, flee also". The idea is that the stimuli produced by the performance of a particular behaviour serve as triggers for others to behave in the same way. Possible examples of contagious behaviour include flight responses, movements in flocks or shoals, and chorusing by birds, frogs, and dogs. Laughing and yawning are good examples of contagious behaviour in humans. Zentall (1996) argues that contagious behaviour must have a genetic basis, i.e. it must involve the triggering on of the instinctive response.

Social facilitation, in its wide meaning is defined as an enhancement of performance of definite behaviour when another person is present. Originally, the theory of social facilitation was intended by Zajonc (1965) to explain the effects of an audience on human performances. The presence or action of the demonstrator might affect the motivation state of the observer that eventually leads to better performance. Recently many authors consider social facilitation a basic form of social learning that can explain by more mundane means some phenomena that have been earlier treated in terms of "animal culture" such as milk bottle opening by tits and potato washing by Japanese macaque monkeys. We will further consider these examples in details.

Stimulus enhancement (Spence, 1956; Galef 1988) is said to have occurred when the presence of an individual draws an observer's attention to a particular object, thus enhancing the observer's opportunity to learn about the object. The result of this narrowing of behavioural focus is that the individual's subsequent behaviour becomes concentrated upon these key variables. The observer does not copy actions of the demonstrator, and the actual actions of the observer are acquired on the basis of trial and error.

Social facilitation and stimulus enhancement from more experienced individuals can serve as proximal mechanisms fostering safe incorporation of novel foods, spread of knowledge about predators and other dangers, and even increasing effectiveness of mate choice.

Observational conditioning takes place when the demonstrator's actions provide the observer with the opportunities to learn that the appearance or movement of an object signals the occurrence of an appetitive or aversive event. The observer thus learns the relation between some part of the environment and the reinforcer, that is, a Pavlovian association may be established (Zentall and Levine, 1972). Socially-transmitted food preferences (Galef, 1988) represent a special case of observational conditioning. The mechanisms responsible for socially-acquired food preferences appear to have strong simple associative learning components (e.g., learned safety or the habituation of neophobia to the novel taste), for which the presence of a conspecific may serve as a catalyst. Furthermore, these specialised mechanisms may be unique to foraging and feeding systems.

One of the best examples of observational conditioning is in the acquisition of fear of snakes by laboratory-reared monkeys exposed to a wild-born conspecific in the presence of a snake. In their experiments Mineka and Cook (1988) showed that lab-reared rhesus monkeys can acquire a fear of snakes by observing other monkeys expressing fear of snakes. When non-fearful lab-reared monkeys were given the opportunity to observe a wild reared demonstrator displaying fear of live and toy snakes, they were rapidly conditioned to fear snakes. The fear response was learned even also in those cases when the fear-demonstrating monkey was shown on a videotape. Then the most intriguing stage of experiments followed. Videos were edited so that identical displays of fear in the demonstrating monkey were modeled in response to toy snakes and flowers, or to toy crocodiles and toy rabbits. The lab-reared monkeys showed substantial conditioning to toy snakes and crocodiles, but not to flowers and toy rabbits. These results provide a strong support for selective (guided) learning which is probably based on a specialized behavioural module. This study also illustrates how observational conditioning occurs. Presumably, a fearful conspecific serves as the unconditioned stimulus, and the snake serves as the conditioned stimulus. It appears that exposure to a fearful conspecific or to a snake alone is insufficient to produce fear of snakes in the observer.

When observation of a demonstrator allows an animal to learn how the environment works, a form of learning is involved which has been labelled "emulation" (Tomasello et al., 1987). Whereas stimulus enhancement changes the salience of certain stimuli in the environment, emulation changes the salience of certain goals (Byrne, 2002). In "emulation" the learner gains information from observing a demonstration, but in achieving the same goal, may use a different method. The investigation which prompted the recognition of this process involved chimpanzees learning from a trained conspecific how to rake food items into a cage (Tomasello et al., 1987). The data showed that chimps exposed to the skilled demonstrator learned how to use the rake, unlike controls, who were unsuccessful in the task, despite manipulating the tool just as often. Animals, however, did not copy the precise strategy employed by the trained conspecifics. Instead, the observers were learning from the demonstration the "affordances" of the tool. The meaning of "emulation learning" (Call and Tomasello, 1994) has expanded to incorporate observational learning about the properties of objects and potential relationships among them. Emulation can also account for findings of observation learning that have been earlier treated as imitation.

Ecological aspects of social learning

Opportunity for the exchange of information among individuals is one of important benefits of living in groups. Species differ in their abilities to use socially acquired information and, in particular, in their abilities to learn through traditions. Members of social groups often monitor the behaviour of their companions in an attempt to gain information about the location of foraging sites or approaching predators. In many cases, for group living animals the only socially acquired information available to individuals is the behavioural actions of others that expose their decisions, rather than initial stimuli on which these decisions are based. So an individual has to make a choice between possibilities to use socially generated cues or to rely on a personal decision basing on the stimuli that gained directly from its environment. A readiness to pay attention only to socially generated cues can reflect a level of conformity of an individual or of a whole group.

A role of social learning in foraging. The idea that animals may observe others to get information about resource quality arose mostly in foraging context (for a review see: Danchin et al., 2004). Animals can use socially gained cues in the context of searching patchy distributed food or making decision about food availability and appropriateness.

Social facilitation of eating novel food has been found in many species. Animals living in groups monitor each other every moment of their periods of activity and react on specific motions which send messages that food is available. For

example, Brown and Laland (2002) have shown that the specific darting motion serves a cue to naive fish to learn to forage on novel prey items. They found that 100% of the individuals that paired with pre-trained fishes learned to accept the novel prey. Naive fishes paired with equally naive individuals actually performed worse (50%) than the individuals learning in isolation (73%).

It is easier for many species to acquire food preference socially than to learn by themselves to avoid food that is poisonous. In Galef et al.'s (1985) elegant experiments with rats some of the critical features of the social interactions preceding formation of food preference have been revealed. The experimenters used a simple apparatus to allow one rat to smell food on an anaesthetised demonstrator rat. An observer rat was placed into the basket of the apparatus, and an anaesthetised (and thus unintentional) demonstrator was placed into a wire mesh basket. Some demonstrators had food dusted on their faces, and others had food placed directly into their stomachs through a tube. In both cases the observers subsequently showed a preference for the flavoured diet that had just been fed to the demonstrator. However, if the rear end of the demonstrator was dusted with food and placed foremost in the basket, then only a slight preference for the food was demonstrated. Finally, if a wad of cotton wool, rather than a rat, was placed in the basket, then despite being dusted with food, there was no change in the attractiveness of the food. Thus the demonstrator does not need to be active to encourage the development of a food preference in another rat. But the demonstrator should be a rat, and the observer must be sure that the demonstrator touched the food by its face, not by a tail!

In experiments with domestic hens Sherwin et al. (2002) have demonstrated that avian social learning should be not fundamentally different that of mammals, and the similar features of the social interactions influence food preference in these groups of animals. In particular, it turned out that the more enthusiastically a demonstrator pecks novel food items, the more items observers consume.

Mate choice copying. It is an intriguing question to what extent social factors can influence the choice of sexual partner. Female mating decisions are often influenced by exposure to the mating interaction of others. This style of mating behaviour is called "mate choice copying" which is said to occur when the probability of an individual selecting another as a sexual partner increases because other individuals (of the same sex) have selected the same partner. Mate choice copying has been reported in several species of birds and fishes. To estimate the role of social information in mate choice, it is necessary to separate the signals deliberately produced by displaying males from the cues that are inadvertently produced by females that make their choices.

Dugatkin (1992) has elaborated an experimental paradigm to investigate this problem. In his study on guppies two males were secured at the ends of an aquarium, one with a demonstrator female nearby. The observer, another female, placed centrally, watched the other female interact with one of the males. When, after the demonstrator has been removed, the observer was allowed to choose between the two males, she consistently chose the male that the first female chose. Multiple comparisons with choices that were made by control females enabled researchers to suggest that females follow a rule: "if this male is good for another female, he is good for me", that is, they utilise the presence of the female near a male as an indication of his quality (for a review see: Brown and Laland, 2003).

Galef and White (2000) have suggested an interesting experimental technique in order to explore social influences on reproductive behaviour. They used Japanese quail (*Coturnix japonica*) as a model species. Researchers changed typical look of birds by adding them a novel trait, namely, a white hat. Females that observed that males with novel traits mated successfully preferred males that possess similar white hats.

These studies show that mate preference can spread rapidly through population by social mechanisms, affecting the strength of sexual selection.

Public information about danger. Acquiring information about danger such as predators by use of social cues can sufficiently decrease the level of lethal risk for group living animals. Utilising information gained from observing conspecifics is especially advantageous as it allows adopting appropriate behaviours without the need to independently verify the approach of a predator.

The general tendency to copy flee-responses of an entire group (flock, herd, or shoal) is based on a simplest form of social learning, namely, on contagion. A panic reaction of a single individual can trigger similar reactions of other members of the group. Individuals react to the flight response of neighbours rather than directly to the advancing predator itself. Synchronous predator responses seem to be cooperative at least in some species. For example, in herrings' schools, attacks from predatory fish and killer whales induce massive predator-response patterns at the school level, including bend, vacuole, hourglass, pseudopodium, herd, split, and "tight-ball" formation within the shoal (Axelsen et al., 2001).

Many researchers reported social learning at a group level when, after observing predator responses of a neighbouring group, a school of fishes or a flock of birds react much more readily to the approach of a predator. For example, minnows showed a significant increase in the frequency of flight responses after observing the flight responses of minnows in a neighbouring tank that had been threatened by a predator (Magurran and Higham, 1988).

Cognitive aspects of social learning

Thorndike's (1911) winged (but disputable) words "Apes badly ape" generate a series of questions such as "Do monkeys ape?" (Visalberghi and Fragaszy, 1990); "do rats ape?" (Byrne and Tomasello, 1995); followed by Tomasello's (1996) revision "Do apes ape?" to which I have added "Do ants ape?". All these questions are derived from a discussion about which, if any, form of social learning is more intelligent. In particular, Whiten (2000) asks a question: Which is more intelligent? Imitation or emulation?

There is a growing body of evidence in literature that observational learning, irrespective of whether it includes imitation or "only" emulation or stimulus enhancement has cognitive implications. It is generally assumed that imitation is a more sophisticated cognitive process. It first of all concerns imitative translation process which includes cognitive implications of how organisms view the behaviour of others, relative to their own behaviour. It implies the ability to take the perspective of another. For this reason, researchers have tried to distinguish imitation from other kinds of social learning and influence. Recent reviews (e.g. Tomasello and Call, 1997) have concluded that only humans, or in some cases chimpanzees, can truly imitate. Emulation also demands feats of intelligence as it implies that the learner can select from the model's performance just the new information it needs, and then efficiently combine this information with its own practical knowledge to deal with the task in its own way.

There are several experimental paradigms for comparative studying cognitive aspects of social learning. A paradigm that is known as "do-as-I-do" test allows testing imitation as a process especially demanding variety of visual cross-modal performance (Heyes, 1993). Virginia and Keith Hayes (1952) gave intensive training to Viki, their young chimpanzee. They taught her by using an imitation set: whenever Vicki responded to the order "Do this, Vicki" by imitating the experimenter's actions, she was rewarded. Viki learned to respond correctly to the command "Do this!" over a broad class of behaviour. More recently, Custance, Whiten, and Bard (1995) replicated this result under more highly controlled conditions. The establishment of a "do as I do" concept not only verifies that chimpanzees can imitate, but it also demonstrates that they are capable of forming an imitation concept (Zentall, 2003).

An instrumental method that gives wider possibilities for comparative studies of social learning is known as the two action method, or two-ways action/one outcome as there are two possible actions which can be performed on one object. Imitation can therefore be tested by finding out whether subjects tend to perform whichever of the two actions they have seen. This can control for displays of other types of social learning such as stimulus enhancement and emulation. This method was first applied by Thorndike (1911) in his studies on chicks. Thorndike noted that those chicks which had a possibility to observe how their companions escape from a puzzle-box, coped with this task faster. He then divided demonstrating chicks into two groups, and trained each of two groups to escape by two different ways. Both ways were available for the observers. They, however, chose that way which they had seen from their demonstrator. This method has been developed in many studies. For example, Dawson and Foss (1965) trained budgerigars, *Melopsittacus undulatus*, to remove a lid from a cup using either their beak or their foot. When naive budgerigars were allowed to observe one of these techniques they showed a significant tendency to use the same method as their demonstrator.

More recently, the two-ways action/one outcome paradigm was successfully used to show evidence of observational learning in many species, such as monkeys, rats, ravens and some others.

In order to examine cognitive aspects of more complex, sequence imitation, experimenters combine the two-ways action/one outcome paradigm with the use of artificial fruit, that is, a device that should be opened for food reward. To open the fruit, several defences have to be removed, as happens in many natural foods used by many species, especially, by primates and parrots. The artificial fruit may be of different levels of complexities, from a simple plastic container that can be easily opened, say, either by teeth or by extremities, to complex devices equipped with bolts, latches and so on. This combined method offers the possibility of a "gold standard" within comparative imitation research.

The use of the artificial fruit paradigm across different species led to the conclusion that some primates are more skilled imitators than others. In experiments of Whiten et al. (1996) chimpanzees and young children were presented with adult human models opening an artificial fruit in one of two alternative ways. In one experiment the defence consisted of a pair of bolts that had to be either poked out through the back, or pulled out at the front with a twisting motion to open the lid and to gain the edible treat inside. In another experiment a pin was spun round and removed using one of two different methods, after which a handle could be disabled by either pulling it out or turning it to one side, allowing the lid to be opened. Chimpanzees were found to copy the method they witnessed being used to remove the bolts, as did children. However, while the children also imitated the method of handle removal, the chimpanzees did not - all tended to use the same method of pulling out. Thus, in a situation when young children learned a technique with quite high fidelity, chimpanzees did not copy all they witnessed so faithfully. Further studies enabled researchers to suggest that, as it has been already noted before, the capacity for true imitation is restricted to humans and apes only, more precisely, to children and chimpanzees raised in a human environment.

It has been recently shown that autistic children display widely ranging imitation deficit whereas they do not differ from normal children in performance in emulation tests (Heyes, 2001). This enables to consider imitation a part of the normal development in our species which includes predisposition for copying actions of close company. It is interesting to note that cross fostering experiments revealed shifts to foster parents' behaviour just to that extent to what members of adopted species are predisposed for mimicking and imitation. This was clearly demonstrated on birds, and we can also

recall an experiment in which a young fox performed species specific behaviour of his own species with only minor shifts to the behaviour of his foster mother, the dog (Mainardi, 1976). Similar results were obtained with ants raised by members of other species (Reznikova, 2001). As far as human infants are concerned, nobody could think about cross fostering experiments but there are some documentary evidences from abandoned children who grew up together with animals (in most cases, with dogs). These infants copied a number of behavioural acts from their companions: eating by licking, walking on four feet and using sounds similar to those of the dogs (Miklósi, 1999). Meltzoff (1988) argues that humans are genetically predisposed to imitate others, and this predisposition allows us to become an imitative generalists.

Huber and co-authors (2001) have investigated how social learning affects object exploration and manipulation in keas, *Nestor notabilis*. This New Zealand parrot, as the authors note, has been used as an example of curiosity in birds for a century, and its natural habitat is thought to have led to the evolution of extreme behavioural flexibility. Five young keas were allowed to observe a trained conspecific that iteratively demonstrated several techniques to open a large steel box. The lid of the box could be opened only after several locking devices had been dismantled: a bolt had to be poked out, a split pin had to be pulled, and a screw had to be twisted out. The observers' initial manipulative actions were compared with those of five naive control birds (non-observers). Although the kea observers failed to open the box completely in their first attempts, they explored more, approached the locking device sooner and were more successful at opening them. These results provide evidence for effects of social facilitation and both generalised and local stimulus enhancement on object exploration in this species. The obtained data also suggest that the keas definitely learned something during observation. Although their initial attempts did not match the response topography or the sequence of model's actions, the birds' efficiency at unlocking the device seemed to reflect the acquisition of some functional understanding of the task through observation, that is, emulation learning.

There was no evidence of true imitation in keas, and a salient explanation given by the authors is that the kea's propensity for exploration, object play and demolition runs counter to the exact reproduction of movements demonstrated by others. Keas are justly mentioned "chimpanzees among birds". Their dynamic and playful style of life does not coincide with close watching and imitating actions of others. Being attracted by a conspecific to explore a novel object does not necessarily lead to slavish copying but may lead to learning what parts of the object are worth exploring. Together with data on anthropoids, the cited results on parrots enable us to regard emulation learning as being cognitively quite demanding.

It is important for comparative imitation studies that many factors should be taken into account in order not to place a species into a list of "backwards". Among these factors, motivation is of great importance as well as ranking and "self-confidence" of individuals that play roles of demonstrators. For members of personalised animal societies it is important to copy actions of highly ranked individuals. It was taken into account in the Huber et al.'s work on keas cited above: highly ranked birds were appointed as demonstrators. Another example comes from Vanchatova's (1984) study in which imitation behaviour in capuchins *Cebus apella* was clearly demonstrated while in other studies this species were unable to learn to use efficiently a tool they had repeatedly observed being used by others. In Vanchatova's (1984) experiment the monkeys were highly motivated by a nature of a reward, that is, a little mouse to eat instead of items of vegetarian diet, and, what is not less important, it was the dominating individual who was used as a demonstrator.

The Spread of Innovation within Populations

In laboratory studies experimenters create "innovators" by themselves. They choose active and exploratory animals that have high ranks in their groups, train them to solve a problem and after training let them to "inculcate" new knowledge among naive members of social groups. This way of experimental investigation helps to enlighten a process of social learning and to estimate potentials of different species. However, such an approach does not give a possibility to learn how innovations spread within populations in the wild.

It is an intriguing question whether a single prodigy individual or may be several advanced individuals can propagate a new tradition in animal community. To catch sight of the transmission of novel behaviour in groups of animals, detailed observations in natural populations are needed, supplemented by experiments in captivity. Sometimes researchers are lucky to witness the gradual establishment of a new tradition. In the majority of cases described in literature new traditions concern vital situations such as feeding techniques or fear of predators. However, exquisite patterns of social behaviour such as specific modes of grooming or mating rituals can also serve as subjects for discussion.

The ways behavioural traditions spread. The phrase "population-specific behavioural traditions" is used to describe behaviours that have the following properties (Nagell, Olguin and Tomasello, 1993):

1. They are acquired through experience, rather than being innate.
2. They are found throughout a well-defined population.
3. They persist from one generation to the next.
4. They are absent in other populations of the same species.

The spread of novel feeding methods through a population, as a particular case of fixing population-specific behavioural traditions, has been documented for a number of terrestrial and avian species. Two of the most famous cases are milk-bottle top opening by birds in Britain (Fisher and Hinde 1949), and washing sweet potatoes (yams) by Japanese macaques (*Macaca fuscata*) (Kawai 1965). In both cases, the spread was initially thought to be due to imitation, but more recent work has cast doubt on this. Let us consider briefly these two examples together with some analogous studies which appreciate the role of simpler forms of learning than imitation.

Blue tits and great tits in Britain are notorious for their ability to break through the foil tops of milk bottles in order to drink the cream at the top. This skill is believed to have originated in a small group, and its spread to the rest of the population has been attributed to imitation. However, the results from a series of experiments by Sherry and Galef (1984) using black-capped chickadees, suggest that the spread of this habit was promoted by more simple than imitation means of social learning. If a bird should come across a bottle that has already been opened, it will drink the milk. Once it has drunk from the bottle, apparently the bird will be very much more likely to break through the foil tops in the future. Pavlovian conditioning provides one explanation for this outcome. Sherry and Galef (1990) report that their subjects were unlikely to open foil tops when they were tested in isolation. In an attempt to answer the question of how the birds came to open foil tops in the first place, experimenters examined the behaviour of a naive bird that had access to a foil covered container of cream when it could see another naive bird in an adjacent cage. The mere presence of this second bird was sufficient to encourage the first bird to peck at the foil cap and eventually open it. The experimenters consider social facilitation as the main mechanism responsible for the origins and perhaps spread of milk-bottle opening among certain birds. The reasons for social facilitation of pecking in this concrete situation are not fully understood, but the presence of the second bird may serve to reduce fear, or to encourage foraging responses, in the experimental subject.

An example of fixing of behavioural tradition in primates is provided by a group of Japanese macaque monkeys who wash sweet potato (yams) before eating them (Kawai 1965; Itani and Nishimura, 1973). In 1952, on the island of Koshima, scientists were providing a group of 22 Japanese macaques with sweet potatoes dropped in the sand. An 18-month-old female named Imo (note that in Japanese Imo means "potato") found she could solve the problem by washing the potatoes in a nearby stream. Imo's name has become legendary as one of the first personalized innovative animal described in scientific literature. The researchers also scattered grains along the beach. The monkeys had to pick the grains from the sand, one grain at a time. Then Imo threw a handful of sandy grain in the water. The sand sank and the grain floated, making it easy to scoop up. Again, other members of Imo's troop eventually learned how to throw their grain in the water. By 1962, almost all the monkeys in the Koshima troop were observed to be washing their sweet potatoes.

Nagell et al. (1993) have suggested that the spread of this habit is due in part to stimulus enhancement. The attention of a naive monkey can be drawn to a potato when it sees another monkey to pick one up. The naive monkey may then pick up its own potato and for social reasons follow the experienced monkey into the river. At this point, the naive monkey may learn by accident the benefits that accrue from placing the potato in the water.

Indeed, stable embedding of new feeding technique in wild populations does not necessarily mean that there is imitation underlying cultural transmission. Behavioural habits can be based on mechanisms of social learning which are simpler than imitation. For instance, stimulus enhancement explains the acquisition of pine-cone stripping behaviour of black rats. Terkel (1996) found that although naive rats never learned to strip cones unaided, the animals were capable of learning the trick if partially striped cones were provided, and especially so if they were exposed to cones with progressively fewer rows of scales removed. Young rats pay close attention to whatever their mother is eating, and often manage to steal partially-eaten cones from her.

Combination of social facilitation, stimulus enhancement and individual learning are likely to underlie forming of "subcultures", or behaviourally specialised "cultural clans" in animals. There are many examples in literature. For instance, populations of crows in Kamchatka specialise in different techniques of getting food from humans. Some flocks regularly steal alms at cemeteries whereas others track skiers in winter and gatherers of mushrooms in summer stealing food from them when they make stops. Dolphins in Shark Bay show a similar specific foraging specialisation - feeding by humans at Monkey Mia beach - in which not all of the population takes part. This variation appears to be maintained by vertical cultural transmission, since most of the dolphins taking advantage of the feeding are offspring of females which were themselves fed (Smolker et al. 1997); hence the specialisation is likely learned while swimming with the mother. Clans of Norway rats specialise on catching fishes or frogs, stealing fishes from fishing nets, harvesting molluscs, and stealing eggs and chicks from birds' nests. Clans dwelling on different sides of a lake display different techniques of catching frogs. Galef (1985) conducted laboratory experiments simulating his own observation in nature on how Norway rats dive for molluscs. It turned out that young pups are able to adopt this technique from their mothers.

Being lucky to catch first manifestations of novel behaviour within a wild population and then monitoring it during long periods, several researchers have reported on very interesting cases of inculcation of new habits, mainly, feeding technique. For instance, the regular cracking of palm tree nuts with the aid of two stones ("hammer" and "anvil") by Japanese macaques was fixed from the very first case and then monitored for 20 years. During this time, about 80% of population had adopted this method (Huffman and Nishie, 2001). Spread of a novel feeding technique was described in humpback whales (Rendell and Whitehead, 2001). In the southern Gulf of Maine, a novel complex feeding technique,

"lobtail feeding", was first observed in 1981, and by 1989 had been adopted by nearly 50% of the population. Not only new feeding techniques can be transmitted socially. Social transmission can also apply to group-specific vocalizations, courtship displays, and grooming postures and so on (McGrew and Tutin, 1978; McGrew, 2004). How it is to be an innovator. As we have already seen from the analysis of examples of innovative behaviour, the main body of data concerns the use of new food or application of new feeding techniques. Some authors consider the frequency of innovative behaviours, for a given taxonomic group, a useful indicator of its behavioural plasticity and its tendency to use novel means to solve environmental problems.

Lefebvre et al. (1997) collected 322 foraging innovations in avian species from nine British and North American ornithological journals and analysed them in connection with measures of relative forebrain size. Innovations were documented from field studies and included such examples as, for Herring gull, catching small rabbits and killing them by dropping on rocks or, for House sparrow, systematic searching of car radiator grills for insects. The authors found that relative forebrain size in different species was related to innovation frequency in the two zones, the British Isles and North America. It seems that at a taxonomic level of innovative behaviour demands at least relevant brains.

What about characteristic features of innovators at the individual level? What individual dispositions required for becoming innovative? Only little is yet known yet about the starting conditions of innovations. For example, in a study with guppies, *Poecilia reticulata*, in which fishes had to quickly make a choice between holes in a partition of an aquarium, Laland and Reader (1999) found that females were more likely to innovate than males, smaller fish more likely than larger fish and food-deprived fish more likely than non-deprived.

The expression of individual behavioural and physiological phenotypes or coping styles is defined as the way to cope behaviourally and physiologically with environmental and social challenges. The existence of different coping styles could be shown for various animal species including humans (Broom, 2003). In mice and rats, for example, aggressive individuals ("proactive copers") entrained more rigid routines, spent less time exploring novel environments and were less alert to changing stimuli in known environments than less aggressive individuals ("reactive copers"). Similar patterns were found in many species such as great tits, domestic pigs, cichlid fish, and others (see Broom, 2001, for a review). In ants scouting individuals that can first solve complex searching problems and usually attract foragers to novel objects, have smaller size, more diverse behavioural repertoire, and they are much more agile than other members of their colony (Reznikova, 1982; Reznikova and Ryabko, 1994).

Experimenters at Konrad-Lorenz Research Station in Grunau had investigated the spread of the ability to trigger a food dispenser in a free-living, semi-tame flock of greylag geese, *Anser anser*, for several years (Fritz et al., 2000; Pfeffer et al., 2002). The researchers investigated hormonal and behavioural correlates with the individual's ability to perform operant tasks in hand-raised greylag goslings. Results suggest that becoming an innovator may be contingent upon individual coping styles. A tendency was revealed that males are more successful in coping with new tasks whereas females are biased toward learning by means of stimulus enhancement. Individuals that displayed elements of innovative behaviour possess higher level of corticosterone than conservative geese.

These, yet limited, data enable us to suggest that predisposition to innovative behaviour is based on some definite genetic features. In changeable environment wide spectrum of adaptations is tested for defects and this includes behavioural adaptations. As McGrew (1992) noted, in many situations when researchers fixed innovations within populations, they could be predicted basing on essential change in environment such as shortage in food, forced migrations and so on. Under such circumstances new customs "invented" by few innovators can be more useful and adequate than species specific stereotypes that had been valid before. However, this does not mean that members of community will readily copy the novel life style. Usually animals observe odd behaviour of their conspecific curiously but keep aloof. Do innovators try to spread new behavioural pattern, in other words, can animal teach each others?

Can animals teach? Active tutoring ("teaching") can be considered the most complex form of sharing knowledge in animal communities. A working definition of teaching widely accepted among students of social learning was suggested by Caro and Hauser (1994): "An individual actor (A) can be said to teach if it modifies its behaviour only in the presence of a naive observer, B, at some cost, or at least without obtaining an immediate benefit for itself. A's behaviour thereby encourages or punishes B's behaviour, or provides B with experience, or sets an example for B. As a result, B acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do, or that it would not learn at all".

There are two main processes of transferring information within populations in which tutoring can be involved: (1) polishing of species-specific behavioural patterns and (2) spreading of innovations. Both processes are parts of social learning. Back-fitting of species-specific behaviour by efforts of tutoring parents is quite usual in animals, first of all, in vertebrate predators. In many species polishing of searching and hunting behaviour makes up an integral part of their ontogenetic development.

However, tutoring as an instrument for spreading innovations is a rare phenomenon in wild life. One can say that this concerns a level of complexity which is over and above the "general plan" of species-specific behaviour. The fact is that innovations can spread within populations by means that are simpler than tutoring. We have already seen this from previous sections and will consider in the last section of this chapter. Although the real role of tutoring is not great,

the analysis of teaching in animals is very important for estimation of limits of their cognitive abilities. Even isolated observations on instances of teaching in the wild are valuable.

There is a large body of data about how predators teach their offspring to kill victims. This concerns predators of different sizes and styles of hunting, from giant whales to little jerboas. At the same time, it is known that members of many species grow up as self-made hunters. For instance, polecats (*Putorius putorius*) learn very quickly how a mouse must be grasped by the neck so that it cannot bite back. During normal ontogenesis complex hunting behaviour can mature with the assistance of individual experience. It can be considered a complex process because innate releasing mechanisms mature as well and they become increasingly more selective through individual learning. This scenario is widely distributed in animal species which can be illustrated by Eible-Eibesfeldt's (1970) examples of the prey catching behaviour of toads, frogs and others. Even in such advanced hunters as Mustellidae parents' instructions have little part. If so, is that necessary for predators to teach the young? Is it possible that parents' instruction run idle in animals? Special investigation is needed in each case if we want to know whether parents take part in shaping of a character of a wild hunter. Let us consider several examples.

It has been known for a long time that in felids and other carnivores' mothers modify their predatory behaviour in a series of stages. It was described by Leyhausen (1979) in domestic cats *Felis catus*. Adult females pursue, capture, kill and eat prey in a smooth sequence with little hesitation between acts. However, when cats become mothers and their kittens start walking out of the nest, mothers alter their behaviour and carry prey to their kittens to eat it in front of them. Next, they carry live prey directly to their offspring and allow them to play with it but recapture it if it escapes. Finally females take little part in prey catching at all, merely moving toward prey initially while kittens chase, capture and dispatch it efficiently. Mothers give characteristic mewing calls to their kittens in all of these situations.

The sequence of mothers' acts is so logical from a human point of view that it undoubtedly looks like successive shaping of the young's hunting behaviour. Under controlled laboratory conditions Caro (1981) tested the alternative hypothesis about the role of mother's teaching in shaping hunting behaviour in kittens. In Caro's study kittens between the ages of 4 and 12 weeks were exposed to domestic mice as a live prey. In one series of trials mother cats were present, while in other trials the mothers were absent. Control kittens received identical exposures but without their mothers being present. Behaviour of mothers was also recorded. The obtained results suggest that maternal behaviour reduces the age at which kittens acquire predatory skills. For instance, when six month-old kittens were tested on their predatory abilities, experimental subjects delivered significantly more bites to the nape but not to other regions of the mouse's body than did control kittens, that is, they more easily applied the method by which adult cats dispatch rodent prey. However, Caro (1981) found it hard to say whether maternal behaviour is sensitive to developmental changes in kitten behaviour. These two processes seem to go in two parallel courses. Indeed, the timing of each step in the mothers' predatory sequence might not be contingent upon improvement in their cubs' predatory skills, but rather change according to their individual time course. Certain mothers started to leave prey with their kittens at very early stages when the young were not able to react to it. Many aspects of mother's predatory behaviour were significantly negatively correlated with increasing skills of their offspring. Caro (1987, 1994) then has continued with studying of interactions between mothers, cubs and prey on wild cheetah in the Serengeti National Park, Tanzania. The researcher found a very slow progress in young cheetah's education seemingly as a graduate result of maternal great efforts. It turned out that cub's hunting skills remain poor up to and beyond independence from their mother, showing surprisingly little improvement in the ten months after first being introduced to prey. In sum, Caro's data enable us to be careful with the conclusion that this is just maternal tutoring which make cats skilled hunters.

A good example that illustrates how difficult it is to judge about the roles of maturation and investments of parents in shaping of hunting behaviour, is the behaviour of ospreys *Pandion haliaetus*. Meinertzhagen (1954) provided rich description of adult ospreys encouraging their fledglings to catch fishes. At first, the adult perched away from the nest with fish in their talons but would not feed the young, despite their screaming for food, repeatedly flying away with an apparent attempt to encourage the young to follow. On the first day the fledglings did not leave the nest, but on the next two days when the young flew off the nest to a rock, they were fed. On the following day, the young followed the parents to hunt over a lake. Each fledgling caught a fish, carried it toward the young and then dropped it, but caught it again and secured it before it hit the water. After having repeated this many times, one of the young finally caught the fish in a stoop and carried it to the rock to eat it. The less successful sibling now flew to the rock to share the catch, but the parent arrived and literally pushed this offspring off the rock forcing it to take wing again. The process of dropping a fish was repeated until the second fledgling finally caught it and went back to the rock to eat. On the fifth day the same procedure was observed with each fledgling following a parent around and unsuccessfully attempting to catch fish that were dropped for it in midair. When the fish reached the surface, the parents would retrieve it until eventually youngsters descended to the water and picked up the fish. On the seventh day, the adults drove the offspring away from the lake and they were not seen again. So, the period of education took six days.

Seemingly, this study provides a strong evidence of a definite role of parental teaching in the building of the hunting behaviour in osprey. Nevertheless, observations of hand-raised young ospreys showed that they successfully caught fishes within three days to three weeks of being released into the wild, in the absence of parental instruction (Schaadt and Rymon, 1982).

These data enables us to suggest that parental "instructions" run in parallel with maturation of hunting behaviour of young, and that at least one aspect of the use of parental teaching in animals is to awake dormant behavioural patterns; repetition of instructions in mammals and numbers of encounters with successful hunters in ants possibly have a cumulative effect. This does not mean that teaching should be excluded from consideration of ontogenesis of hunting behaviour.

Transmission of innovations by teaching. Active teaching as a mean for sharing new experience would seem to be very rare in animal kingdom, even in apes. The great role of imitation in social life of anthropoids does not necessarily means that they can teach each others. Young chimps learn how to break twigs from trees, strip away the leaves, and insert them into termite holes by observing adults. The steps required to extract termites in this manner are lengthy and complex. Without the demonstrations of adults, many chimps would probably never become very successful termite fishers. However, part of the acquisition of this tool use appears to relate to innate characteristics of chimpanzee behaviour. All young chimpanzees amuse themselves by playing with sticks and poking them into holes. It seems as though the chimps are able to observe the more skilled adults and translate their juveniles play into a successful means for securing food. But this does not mean that young chimpanzees follow instructions of adults (Goodall, 1986).

During ten years of investigations Boesch (1991) observed interactions between mothers and their young among Tai chimpanzees in the context of nut cracking. He divided his observations of mother-offspring inter-relations into "stimulation", "facilitation" and "active teaching". Observations of stimulations and facilitation included such things as mothers' leaving intact nuts for their infants to crack (which they never did for other individuals) or placing hammers and nuts in the right position near the anvil for their infants to use. Stimulations were observed on 387 occasions of interactions between mothers and their children. Stimulation differs from the common behavioural pattern for adult chimpanzees, when they carry their hammers during nut collection and consume the nuts that they have placed on an anvil. Mothers incurred a foraging cost by having to find more nuts and another tool for opening them.

Active teaching was observed only twice and involved direct intervention on the part of the mother in her offspring's attempt to crack open a nut. In one example, a six-year-old male had taken a majority of his mother's nuts, as well as her stone-hammer. After the young male placed a nut on the anvil, but prior to opening it, his mother approached, picked up the nut, cleaned the anvil, and put the nut back in a different position, more suitable for opening. The young male cracked the nut and ate the kernel. In the second example, another mother reoriented the hammer for her five-year-old daughter who then succeeds in opening several nuts by maintaining the same grip on the hammer that her mother had used.

One more example of isolated cases of teaching in animals came from the experimental investigations on free-living scrub jays, *Aphelocoma coerulescens*, by Midford et al. (2000). Experimenters trained models (demonstrators) and then followed them as they modelled the task in the presence of naïve (observer) animals. Jays had to learn that a class of objects (bright plastic rings) indicated the presence of buried food (peanut peaces) in a specific location, the centre of the ring. Birds were trained in their family groups to perform the task during summer season, and were allowed to perform the task in the presence of juveniles in later years. Jays living in 18 control families received partial exposure to the training situation, but received no exposure to the ring before being presented with the task in the presence of their young. Juveniles in 16 families with trained jays were able to witness demonstrations and to scrounge peanut peaces from the models as they completed the task. These 41 juveniles learned much more of the task than the 33 juveniles in control families. What is important for our narrative is that the authors observed three cases of active teaching in two separate families. In each case, the highly ranked bird (the breeder of the family) dug in a centre of a ring until it uncovered the food. Then, rather than taking the pieces of nuts, the adult either departed or stood over the depression it dug, pointed its bill downwards, towards the pieces, until the juvenile took them. This differs markedly from the usual behaviour of jays after finding bits and, as the authors give this, fall within the definition of teaching.

Culture in Animal Societies

In this paragraph we will briefly analyse a complex and fascinating problem of what is culture in animals. The relationship between cultural and genetic evolution was identified by Wilson (1975, 1998) as one of the "great remaining problems of the natural sciences". Several studies, adopting Dawkins' (1976) concept of the "meme" as the unit of cultural evolution, have examined factors influencing the transmission and success of memes in animal cultures. The presence of cultural processes within animal societies is an area of some controversy. How to treat cultural behaviour in animals much depends on its definition. Many definitions in literature attribute cultural traits only to humans. At the other end of the scale is considering culture as a "meme pool" in populations which can include all cases of the regular use of public information in populations basing on very simple forms of social learning.

Many cognitive ethologists agree now that human beings are biologically adapted for culture in ways that other primates are not, as evidenced most clearly by the fact that human cultural traditions accumulate modifications over historical time. Our species is likely to possess some uniquely powerful forms of cultural learning, enabling the acquisition of language, discourse skills, tool-use practices, and other conventional activities.

Not arguing about restricted notions of "culture" in animals, I would rather adhere to broad definitions basing on social learning as the main mechanism of "cultural transmission" of behavioural patterns in animal societies. I see here a

fascinating perspective of estimating limits of power of social learning in non humans that allow some species to improve adaptiveness of behaviour by non genetic means. In this context, I consider the broad definitions as acceptable such as "culture is information or behaviour acquired from conspecifics through some form of social learning" (Boyd and Richerson 1996), and "animal tradition that rests either on tuition of one animal by another or on imitation by one animal of acts performed by another" (Galef, 1992). Defining culture as a package of behaviours, the working description given by Nishida (1987) is useful: "Cultural behaviour is defined as behaviour that is (a) transmitted socially rather than genetically, (b) shared by many members within a group, (c) persistent over generations and (d) not simply the result of adaptation to different local conditions".

Empirical approaches for studying animal culture. The empirical study of cultural processes in animals is generally approached in two major ways: controlled laboratory experiments on mechanisms of social learning and field descriptions of behavioural variation (Lefebvre and Palameta, 1988). Both make important contributions to our understanding of culture.

The first approach focuses on experimental study of the cognitive processes underlying cultural transmission. In general, controlled laboratory experimentation is a preferred methodological tool; this gives the approach the advantage of controlled conditions and hence less chance of ambiguity in the interpretation of data. However, the studies do not necessarily relate to what occurs in the wild.

The second approach is field-based; here culture is deduced from patterns of behavioural variation in time and space, which cannot be explained by environmental or genetic factors (Whiten et al. 1999). This approach has been likened to ethnography in the social sciences, and thus is called "ethnographic approach" in recent ethological literature. Practically, studies of chimpanzees, the most "cultural" after our species, have elaborated the following steps to identify cultural variations: 1) to show that behavioural differences between chimpanzee populations are not consistent with a genetic explanation - for example, where a boundary between different methods of tool use occurs within the range of a sub-species (e.g. at a large river), rather than between sub-species; 2) to check that the behavioural differences cannot be explained by ecological factors such as availability of suitable raw materials for making tools; 3) to study the transmission processes used by animals in controlled experiments: can they learn by watching others? If so, what kind of things do they learn? Well designed experiments of this kind can guide researchers to the most likely learning mechanisms at work in the wild.

"Hearths of culture" in animal societies. We argue about cultural changes in animal societies in those cases when animals learn new living habits and pass them along to the next generation. In such a situation spread of a certain innovation results in stable conservation of a new custom that is further maintained and transmitted in a train of generations through social learning. Culture thus is displayed as the presence of geographically distinct variants of habits. Even in this limited sense, culture was long considered to be a uniquely human trait. Ethologists have investigated the problem of animal culture for decades but only in the last few years a clear picture of cultural diversity in several "elite" species begun to emerge. Insight into cultural evolution came from comparative geographic approach when researchers have thoroughly studied behavioural customs in different populations and thus revealed "hearths of culture" in animal societies.

The main methodological difficulty on the way of studying animal culture is to recognize innovations in the field. Even when the origin of a certain innovation had been observed, it is difficult to predict a living trajectory of this innovation. As it has been noted earlier in this chapter, innovations can be spread by means of relatively simple forms of social learning and even low-end innovations can lead to extensive cultural change. Remember Japanese macaque potato washing. By using the water in connection with their food, the Koshima monkeys began to exploit the sea as a resource in their environment. Sweet potato washing led to wheat washing, and then to bathing behaviour and swimming, and the utilization of sea plants and animals for food (Kawai, 1965).

At the same time, there are reasons to believe that new skills do not spread easily in animal populations. As Kummer and Goodall (1985) note, of many innovative behaviours observed, only a few will be passed on to other individuals, and seldom will they spread through the whole troop. For example, Goodall (1986) observed two instances of using stones by adolescent chimpanzees to kill dangerous insects. She supposed that usage of stones should become customary in that reference group. But this had not happen in the following thirty years, the innovation faded away.

The chimpanzee is clearly the most interesting animals from a cultural point of view. Different populations of chimpanzees seem to have their own unique behavioural repertoires, including such things as food preferences, tool use, gesture signals, and other behaviours, and these group differences often persist across generations. After collecting a great body of data in the wild, the first intimation that chimpanzee possess "material culture" came with McGrew's (1992) book about chimpanzee's tool use. Since then, new observations have appeared and some researchers have argued that individual communities of chimpanzees have their own local traditions. The grand synthesis was done by a collective of primatologists published in Nature (Whiten et al., 1999; see also a review by de Waal, 1999).

The researchers discovered the various habits of chimpanzees at seven field sites and clearly distinguished 39 culturally transmitted behavioural patterns. Some of them concern tool use, such as ant dipping, termite fishing, nut cracking, honey dipping, drinking water with leaves, and so on. Others concern characteristic behavioural habits such as rain-

dances, hand-clasp grooming, details of courtship rituals, and so on. For example, some populations fish for ants with short sticks, eating insects from the stick one by one. Only in one population apes developed the more efficient technique of accumulating many ants on a long rod, after which all insects are swept into the mouth with a single hand motion. Another impressive difference concerns leaf-using for drinking water. In different communities chimpanzees use "leaf sponge" crumbling leaves in their mouth, soaking them in tree hollows with their hands, and sucking the water from them. The other type is "leaf spoon" where apes use leaves like a spoon, without crumbling them up, to scoop out the water.

Until recently chimpanzees were considered the only species among great apes that possess elements of "material culture". Nowadays researchers consider chimpanzees displaying the highest level of manufacturability but not a single species sharing with human the membership in the club of animals with culture. Besides Africa's gorillas and chimpanzees great apes include orangutans, the fabled red apes of the forests of Indonesia. Orangutans *Pongo pygmaeus* are less social than other primates, living a rather solitary life in the wild. They are slow in movement, not leaping vigorously from limb to limb like chimps or crashing through underbrush like the gorilla. Thirty years of field observations of the shy Southeast Asian orangutan allow the international group of researchers to conclude that these apes definitely have the ability to adopt and pass along learned behaviours (van Schaik et al., 2003).

Studying six populations of orangutans in Borneo and Sumatra, Indonesia, researchers identified 24 examples of behaviours that have been defined as cultural variants. Many of the culturally transmitted behaviours involve tool use such as using sticks to dig seeds out of fruit, to poke into tree holes to obtain insects, or to scratch; using leaves as napkins or as gloves to protect against spiny fruit. Twelve other behaviours, such as making a pillow with twigs, were seen only rarely or were practiced by only a single individual. The practices common in one group and absent in another are of great interest to researchers because variations on these behaviours found among the different populations seem to be cultural. For example, in a Sumatran swamp, one particular group of orangutans like a fruit that was protected by needle-like spines, and to get to the edible seeds inside, the apes used a tool. With a sharp stick, they pried open the fruit to extract the seeds. Only a single group of the six observed has discovered how to use sticks to extract insects from tree holes or to wedge out seeds from fruits. Such tool use is common among chimpanzees, but the Sumatran orangutan band puts a unique twist to the practice - they grip the stick with their teeth instead of their hands. On the far side of the river another group of orangutans have plenty of sticks available, but they do not use them on fruit; most ignore the fruit, others smash it to get the seeds. The stick trick seemed to be an invention created by one group that was passed along. This is what researchers call "a cultural boundary".

Recent data obtained by Krützen et al. (2005) allow adding marine mammals to the catalog of culturally transmitted forms of tool use in nonhuman populations. In Shark Bay, Western Australia, wild bottlenose dolphins (*Tursiops* sp.) apparently use marine sponges as foraging tools. Sponge carrying came to the attention of scientists 20 years ago when a boater reported seeing a dolphin in Shark Bay with a "tumor" on its beak. The tumor turned out to be a sponge, and in 1997 researchers proposed sponge carrying as the first known example of tool use in dolphins (Smolker et al., 1997). Dolphins have devised a way to break marine sponges off the seafloor and wear them over their snouts when foraging. Researchers believe that dolphins use sponges as a kind of glove to protect their sensitive rostrums when they probe for prey in the substrate. Unlike in apes, tool use in this population is almost exclusively limited to a single matriline that is part of a large albeit open social network of frequently interacting individuals. The researchers conclude that the behaviour is culturally transmitted, presumably by mothers teaching the skills to their sons and daughters, although they have not actually observed this feat in action.

Tool-use is the most amazing but not a single population-specific behavioural trait enabling cetacean biologists to claim that marine mammals possess culture (Whitehead, 1998; Decke et al., 2000) or at least traditions. Field researchers listed many population-specific patterns concerning foraging strategies, styles of diving and other behavioural traits many of them have been clearly demonstrated as transmitted by means of social learning (for a review see Mann et al., eds., 2000).

Conclusion

Social learning plays an important role in the processes of "tuning" behaviour in group living species and in those which live solitary but at least have contacts with relatives at early stages of ontogenesis. Readiness to gain information from conspecifics reflects both the conformity prevailing in animals' society and the flexibility that enables animals to improve their individual behaviour in changeable environment.

Capabilities of learning from others and about others allow members of species to decrease the cost of being equipped by inherited suite of a great number of behavioural characteristics. Being extra guided by means of social learning, animals can increase their fitness and make relationships with their environment more flexible and thus more adequate. It is possible that social learning has more fundamental importance as a part of evolutionary strategies of many species than we thought before.

Animals' ability to develop completely new behaviour by observing innovations invented by a single or a few advanced individuals should be based on intelligence rather than automatic population processes. Effectiveness of new behaviours

performed by "wild prodigies" may be evident for conspecifics but this does not mean that many imitators will subscribe to the same activity. Usually animals observe innovators and try to stand aside. Innovations are most often extinguished within a viscous environment of wild minds. One can say that non-humans badly teach and poorly learn, and that preparedness is the best teacher for animals.

It is very likely that, as Premack and Premack (1996) give this, humans possess unique "pedagogic disposition" to exploit the learners' "predisposition to culture", for teachers to demonstrate correct performance for the benefit of the learner.

In general, social learning is based on difference between members of animal communities, that is, on behavioural specialisation in populations, and in some situations, on cognitive specialisation of individuals.

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