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Twelve Misunderstandings of Kin Selection

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Abstract

Hamilton's theory of kin selection is much misunderstood. This paper lists and refutes 12 of the commonest misunderstandings, for example: "Kin selection is a special, complex kind of natural selection, as opposed to 'individual selection'"; "Kin selection is a form of group selection"; "All species members share the majority of their genes, so selection should favour universal altruism", "Kin selection only works for rare genes", "Individuals should tend to inbreed, simply because that brings close relatives into the world". The exposing of common errors such as these is a constructive, not a destructive, exercise.

Introduction

Kin selection (Hamilton 1963, 1964 a, 1964 b, 1970, 1971, 1972, 1975, 1979; Maynard Smith 1964) has become a bandwagon, and when bandwagons start to roll attitudes sometimes polarise. The rush to jump on provokes a healthy reaction. So it is that today the sensitive ethologist with his ear to the ground detects a murmuring of sceptical growls, rising to an occasional crescendo of smug baying when one of the early triumphs of the theory encounters new problems. Such polarisation is a pity. In this case it is exacerbated by a notable series of misunderstandings, both on and off the kin selection bandwagon. Many of these misunderstandings arise from secondary attempts at explaining Hamilton's ideas rather than from his original mathematical formulation. As one who has fallen for some of them in my time and met all of them frequently, I would like to try the difficult exercise of explaining in non-mathematical language 12 of the commonest misunderstandings of kin selection. The 12 by no means exhaust the supply. See, for instance, Grafen (1979, in press) for good exposés of two other, rather more subtle ones. The 12 sections can be read in any order.

Misunderstanding 1:

“Kin selection is a special, complex kind of natural selection, to be invoked only when ‘individual selection’ proves inadequate”

This one logical error, on its own, is responsible for a large part of the sceptical backlash that I mentioned (e.g. Grant 1978 and other examples cited in Dawkins 1978). It results from a confusion between historical precedence and theoretical parsimony: “Kin selection is a recent addition to our theoretical armoury; for many purposes we got along quite well without it for years; therefore we should turn to it only when good old fashioned ‘individual selection’ fails us”.

Note that good old-fashioned individual selection has always included parental care as an obvious consequence of selection for individual fitness. What the theory of kin selection has added is that parental care is only a special case of caring for close relatives. If we look in detail at the genetical basis of natural selection, we see that ‘individual selection’ is anything but parsimonious, while kin selection is a simple and inevitable consequence of the differential gene survival that, fundamentally, *is* natural selection (Williams 1966, Dawkins 1976, 1978). Caring for close relatives at the expense of distant relatives is predicted from the fact that close relatives have a high chance of propagating the gene or genes ‘for’ such caring: the gene cares for copies of itself. Caring for oneself and one’s own children *but not* equally close collateral relatives is hard to predict by any simple genetic model. We have to invoke additional factors, such as the assumption that offspring are easier to identify or easier to help than collateral relatives. These additional factors are perfectly plausible but they have to be *added* to the basic theory.

It happens to be true that most animals care for offspring more than they care for siblings, and it is certainly true that evolutionary theorists understood parental care before they understood sibling care. But neither of these two facts implies that the general theory of kin selection is unparsimonious. If you accept the genetical theory of natural selection, as all serious biologists now do, then you must accept the principles of kin selection. Rational scepticism is limited to beliefs (perfectly sensible ones) that *in practice* the selection pressure in favour of caring for relatives other than offspring is unlikely to have noticeable evolutionary consequences.

There is a sophisticated population geneticists’ version of Misunderstanding 1. “We don’t have to take the theory of kin selection seriously, because population geneticists have not yet worked out a complete mathematical model of it.” Even if the premise of this argument were true (see Charnov 1977) the interesting point is this. Whatever shortcomings may have surfaced in the mathematical theory of, say, sibling care, will almost certainly apply to parental care too. Population geneticists have happily swallowed parental care for years, and it is only when it is pointed out that parental care

is just a special case of something less familiar that they start worrying about the theory. If there are indeed serious problems with the theory of kin selection (which I doubt), it is a virtue of the new part of the theory that it has called attention to problems which must all along have been present in the old theory of parental care. The irony is that some sceptical geneticists are suspicious of the new, without realising that their old theory of parental care must be tarred with the same brush.

Charlesworth (1978, PP. 317—318), explicitly contradicts this. He rightly says that some people wish to suggest “that altruism among sibs is as likely to evolve as parental care, since offspring and parents have the same degree of relatedness as full sibs”.

Charlesworth goes on “What is left out of such an argument is that the cost/benefit ratios are expressed in terms of fitness, and the number of offspring raised successfully is a component of the parents’ fitness”. With great respect I suggest that Charlesworth is applying the standard methodology of population geneticists (treating offspring as a measure of fitness) while forgetting the fundamental principle underlying this methodology (offspring are vehicles of parental genes, but, then, so are siblings).

Charlesworth’s remarks come at the end of an important, and rightly influential (Parker 1978), paper in which he makes the following point. If a gene for sibling altruism has full penetrance, those members of a clutch or litter who possess it will tend to sacrifice themselves for those who do not. Therefore the gene will disappear from the population unless we conceptually save it by assuming low penetrance. This is a good point, but in principle it applies to the parent/offspring relationship too. The reason it does not in practice occur to us when we think of parents and offspring is that the parent/offspring relationship is marked by a strong practical asymmetry: we do not expect offspring to sacrifice themselves for their parents anyway, because they are smaller and more helpless. But the same practical asymmetry could apply to a sibling relationship. A sibling who acts as a ‘helper at the nest’ (Brown 1975) is always older than the nestlings he feeds. The asymmetric strategy (Maynard Smith and Parker 1976) ‘feed young nestlings in the nest from which you have just fledged’ is no more subject to Charlesworth’s problem than ordinary parental care is. Charlesworth’s problem arises in any symmetrical relationship. The difference between the parent offspring and the sibling relationship is that the latter can be symmetrical while the former cannot.

Misunderstanding 1 has perhaps been unwittingly encouraged by an influential definition of kin selection: “The selection of genes due to one or more individuals favoring or disfavoring the survival and reproduction of relatives (other than offspring) who possess the same genes by common descent” (Wilson 1975, P.587). I am glad to see that Wilson has omitted the phrase ‘other than offspring’ in his more recent definition, in favour of the following: “Although kin are defined so as to include offspring, the term kin selection is ordinarily used only if at least some other relatives, such as brothers, sisters, or parents, are also affected” (Wilson 1978, P.219). This is undeniably true, but I still think it is regrettable. Why should we treat parental care as special, just because for a long time it

was the only kind of kin-selected altruism we understood? We do not separate Neptune, Uranus and Pluto off from the rest of the planets simply because for centuries we did not know of their existence. We call them all planets because they are all the same kind of thing.

At the end of his 1975 definition, Wilson added that kin selection was “One of the extreme forms of group selection”. This, too, has happily been deleted from his 1978 definition. It is the second of my 12 misunderstandings.

***Misunderstanding 2:
“Kin selection is a form of group selection”***

Group selection is the differential survival or extinction of whole groups of organisms (Maynard Smith 1976). It happens that organisms sometimes go around in family groups, and it follows that differential group extinction could turn out to be effectively equivalent to family selection or ‘kin group selection’ (Hamilton 1975). But this has nothing to do with the essence of Hamilton’s basic theory: those *genes* are selected that tend to make individuals discriminate in favour of other individuals who are especially likely to contain copies of the same genes. The population does not need to be divided up into family groups in order for this to happen, and it is certainly not necessary that whole families should go extinct or survive as units.

Animals cannot, of course, be expected to know, in a cognitive sense, who their relatives are (see Misunderstanding 3), and in practice the behaviour that is favoured by natural selection will be equivalent to a rough rule of thumb such as ‘share food with anything that moves, in the nest in which you are sitting’. If families happen to go around in groups, this fact provides a useful rule of thumb for kin selection: ‘care for any individual you often see’. But note once again that this has nothing to do with true group selection: differential survival and extinction of whole groups do not enter into the reasoning. The rule of thumb would work if there is any ‘viscosity’ in the population such that individuals are statistically likely to encounter relatives; there is no need for families to go about in discrete groups.

Hamilton (1975) is perhaps right to blame the phrase ‘kin selection’ itself for some misunderstanding, ironically since it was coined with the laudable purpose of emphasising its distinctness from group selection (Maynard Smith 1964). Hamilton himself does not use the phrase, preferring to stress the relevance of his central concept of inclusive fitness to any kind of genetically non-random altruism, whether concerned with kin-relatedness or not. For instance, suppose that within a species there is genetic variation in habitat choice. Suppose further that one of the genes contributing to this variation has the pleiotropic effect of making individuals share food with conspecifics whom they encounter. Because of the pleiotropic effect on habitat choice, this altruistic gene is effectively discriminating in favour of copies of itself, since individuals possessing it are especially likely to congregate in the same habitat and therefore meet each other. They do not have to be close kin (Hamilton 1975; D. S. Wilson 1977; but see Charlesworth 1979).

Any way in which an altruistic gene can ‘recognise’ copies of itself in other individuals could form the basis for a similar model. The principle is reduced to its bare essentials in the improbable but instructive ‘green beard effect’ (Dawkins 1976): selection would theoretically favour a gene that pleiotropically caused individuals to develop a green

beard and also a tendency to be altruistic to green-bearded individuals. Again there is no need for the individuals to be kin.

D. S. Wilson (1975, 1977) joins Hamilton in emphasising that selection may favour other kinds of genetically non-random altruism in addition to altruism based on kinship, but he ruins his case by gratuitously insisting on 'group selection' as the heading for his interesting models. His loyalty to the concept of group selection reaches positively foolhardy lengths in one model (Wilson 1977, pp 160—161): he gives a mathematical argument to show that, even in randomly constituted groups, an individual "experiences its own type in greater frequency than is actually present in the deme. This causes types to interact more with similar types than with other types". A startling and exciting result, it might be thought, and the basis for the only workable general model of truly group-selected altruism. But alas, when the mathematical smokescreen is blown away, what is revealed is vacuous: an individual experiences his own type more than other types simple and solely because he *himself* is of his own type, and he obviously 'experiences' himself! That is no basis for altruism. Not all Wilson's models are so trivial, but Maynard Smith (1976) is right that they are NOT models of group selection. Like Hamilton's, they are models of non-random assortment of altruistic genes. Maynard Smith is also surely right that, even if kinship is not quite the only possible basis for such non-randomness, it is the most plausible.

***Misunderstanding 3:
“The theory of kin selection demands formidable feats of cognitive reasoning by animals”***

In a much quoted ‘Anthropological Critique of Sociobiology’, Sahlins (1977, P. 44—45) says the following:

“In passing it needs to be remarked that the epistemological problems presented by a lack of linguistic support for calculating, r , coefficients of relationship, amount to a serious defect in the theory of kin selection. Fractions are of very rare occurrence in the world’s languages, appearing in Indo-European and in the archaic civilizations of the Near and Far East, but they are generally lacking among the so-called primitive peoples. Hunters and gatherers generally do not have counting systems beyond *one*, *two* and *three*. I refrain from comment on the even greater problem of how animals are supposed to figure out how that r [ego, first cousins] = $1/8$. The failure of sociobiologists to address this problem introduces a considerable mysticism in their theory.”

A pity, for Sahlins, that he succumbed to the temptation to ‘refrain from comment’ on how animals are supposed to ‘figure out’ r . The very absurdity of the idea he tried to ridicule should have set mental alarm bells ringing. A snail shell is an exquisite logarithmic spiral, but where does the snail keep its log tables; how indeed does it read them, since the lens in its eye lacks ‘linguistic support’ for calculating μ , the coefficient of refraction? How do green plants ‘figure out’ the formula of chlorophyll? Enough, let us be constructive.

Natural selection chooses genes rather than their alleles, because of those genes’ phenotypic effects. In the case of behaviour, the genes presumably influence the state of the nervous system, which in turn influences the behaviour. Whether it is behaviour, physiology or anatomy, a complex phenotype may require sophisticated mathematical description if we are to understand it. This does not, of course, mean that the animals themselves have to be mathematicians. Unconscious ‘rules of thumb’ of the kind already mentioned will be selected. For a spider to build a web, rules of thumb are required that are probably more sophisticated than any that kin-selection theorists have postulated. If spider webs did not exist, anybody who postulated them might well provoke scornful scepticism. But they do exist; we have all seen them, and nobody wonders how spiders ‘figure’ designs out.

The machinery that automatically and unconsciously builds webs must have evolved by natural selection. Natural selection means the differential survival of alleles in gene pools. There must, therefore, have been genetic variation in the tendency to build webs. Similarly, to talk about the evolution of altruism by kin selection we have to postulate genetic variation in altruism. In this sense we have to postulate alleles ‘for’ altruism, to

compare with alleles for selfishness. This brings me to my next misunderstanding.

Misunderstanding 4:

“It is hard to imagine a gene ‘for’ anything so complex as altruistic behaviour toward kin”

The problem results from a misunderstanding about what it means to speak of a gene ‘for’ behaviour. No geneticist has ever imagined that a gene ‘for’ some phenotypic character such as microcephaly, or brown eyes, is responsible, alone and unaided, for the manufacture of the organ that it affects. A microcephalic head is abnormally small, but it is still a head, and a head is much too complex a thing to be made by a single gene. Genes don’t work in isolation, they work in concert. The genome as a whole works with its environment to produce the body as a whole, just as a whole recipe, if faithfully obeyed, produces a whole cake. You cannot break the finished cake up into its component crumbs and map each crumb on to a particular word or letter of the recipe. But if you *change* one word in the recipe, the cake may come out different as a result. The *difference* between two cakes might well be due to a one word difference in their two recipes.

Similarly, ‘a gene for behaviour X’ can only refer to a *difference* between the behaviour of two individuals. Fortunately, it is precisely such differences between individuals that matter for natural selection. When we speak of the natural selection of, for instance, altruism towards younger siblings, we are talking of the differential survival of a gene or genes ‘for’ sibling altruism. But this simply means a gene that tends to make individuals in a normal environment more likely to show sibling altruism than they would under the influence of an allele of that gene. Is that implausible?

It is true that no geneticist has actually bothered to study genes for altruism. Nor has any geneticist studied web-building in spiders. We all believe that web-building in spiders has evolved under the influence of natural selection. This can only have happened if, at each and every step of the evolutionary way, genes for some difference in spider behaviour were favoured over their alleles. This does not, of course, mean there still have to be such genetic differences; natural selection could, by now, have removed the original genetic variance.

Nobody denies the existence of maternal care, and we all accept that it has evolved under the influence of natural selection. Again, we don’t need to do genetic analysis to convince ourselves that this can only have happened if there were a series of genes for various behaviour differences which, together, built up maternal behaviour. Once maternal behaviour, in all its complexity, exists, it takes little imagination to see that only a small genetic change is required to push it over into elder sibling altruism.

Suppose the ‘rule of thumb’ that mediates maternal care in a bird is the following: ‘feed anything that squawks inside your nest’. This is plausible, since cuckoos seem to have exploited some such simple rule. Now all that is needed to obtain sibling altruism is a

slight quantitative shift, perhaps a small postponement of a fledgeling's departure from the parental nest. If it postpones its departure until after the next brood has hatched, its existing rule of thumb might well cause it automatically to start feeding the squawking gapes that have suddenly appeared in its home nest. Such a slight quantitative postponing of a life-historical event is exactly the kind of thing a gene can be expected to effect (Gould 1977). In any case the shift is child's play compared with those that must have accumulated in the evolution of maternal care, web-building, or any other undisputed complex adaptation. Misunderstanding 4 turns out to be only a new version of one of the oldest objections to Darwinism itself, an objection that Darwin (1859) anticipated and decisively disposed of in his section on 'Organs of extreme perfection and complication'.

Altruistic behaviour may be very complex, but it got its complexity, not from a new mutant gene, but from the pre-existing developmental process that the gene acted upon. There already was complex behaviour before the new gene came along, and that complex behaviour was the result of a long and intricate developmental process involving a large number of genes and environmental factors. The new gene of interest simply gave this existing complex process a crude kick, the end result of which was a crucial change in the complex phenotypic effect. What had been complex maternal care, say, became complex sibling care. The shift from maternal to sibling care was a simple one, even if both maternal and sibling care are very complex in themselves.

To stick my neck out a little, it seems to me that, far from genes for altruistic behaviour being implausible, it may even be that a *majority* of behavioural mutations will turn out to be properly describable as either altruistic or selfish. The argument is a modification of FISHER's (1930) demonstration of the unlikelihood of neutral phenotypic traits

Remember that the words altruistic and selfish are, in this context, defined in terms of *effects*, not motives or intentions. A gene for altruism, then, is any gene that, compared with its alleles, causes individuals to benefit other individuals at a cost to themselves. Consider a pride of lions gnawing at a kill. An individual who eats less than her physiological requirement is, in effect, behaving altruistically towards others who get more as a result. If these others were close kin, such restraint might be favoured by kin selection. But the kind of mutation that could lead to such altruistic restraint could be ludicrously simple. A genetic propensity to bad teeth might slow down the rate at which an individual could chew at the meat. The gene for bad teeth would be, in the full sense of the technical term, a gene for altruism, and it might indeed be favoured by kin selection.

In the light of this reasoning, we may divide all new mutations up into three exhaustive categories: selfish ones whose net effect is to favour the individual at the expense of others; altruistic ones whose net effect is to favour others at the expense of self; and neutral ones whose net effect is neither of these. It is arguable that the neutral category may be rather small, at least if we limit consideration to those mutations that have any

kind of phenotypic effect. In any case, this thought experiment should be sufficient to dispel the belief that the evolution of altruistic behaviour is too complex to result from gene substitutions.

Misunderstanding 5:

“All members of a species share more than 99 % of their genes, so why shouldn’t selection favour universal altruism?”

“This whole calculus upon which sociobiology is based is grossly misleading. A parent does not share one half of the genes with its offspring; the offspring shares one half of the genes in which the parents differ. If the parents are homozygous for a gene, obviously all offspring will inherit that gene. The issue then becomes: How many shared genes are there within a species such as *Homo sapiens*? King and Wilson (1975) estimate that man and chimpanzee share 99% of their genetic material; they also estimate that the races of man are 50 times closer than are man and chimpanzee. Individuals whom sociobiologists consider unrelated share, in fact, more than 99% of their genes. It would be easy to make a model in which the structure and physiology important in behavior are based on the shared 99 % and in which behaviorally unimportant differences, such as hair form, are determined by the 1%. The point is that genetics actually supports the beliefs of the social sciences, not the calculations of the sociobiologists (Washburn 1978, P. 415).

This misconception arises not from Hamilton’s own mathematical formulation but from oversimplified secondary sources to which Washburn refers. The mathematics, however, are difficult, and it is worth trying to find a simple verbal way of refuting the error.

Whether 99% is an exaggeration or not, Washburn is certainly right that any two random members of a species share the great majority of their genes. What, then, are we talking about when we speak of the coefficient of relatedness between, say, siblings as being 50%? We must answer this question first before getting down to the error itself.

The unqualified statement that parents and offspring share 50 % of their genes is, as Washburn rightly says, false. It can be made true by means of a qualification. A lazy way of qualifying it is to announce that we are only talking about rare genes; if I have a gene that is very rare in the population as a whole the probability that my child or my brother has it is about 50%. This is lazy because it evades the important fact that Hamilton’s reasoning applies at all frequencies of the gene in question; it is an error (see Misunderstanding 6) to suppose that the theory only works for rare genes. Hamilton’s own way of qualifying the statement is different. It is to add the phrase ‘identical by descent’. Siblings may share 99% of their genes altogether, but only 50% of their genes are 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.

So, we have identified two ways of explaining the meaning of r ; the coefficient of relatedness: the 'rare gene' way and the 'identical by descent' way. Neither of these, however, shows us how to escape from Washburn's paradox. Why is it not the case that natural selection will favour universal altruism, since most genes are universally shared in a species? I think the simplest way to explain it is by using Maynard Smith's (1974) language of evolutionarily stable strategies.

Let there be two strategies, Universal Altruist U, and Kin Altruist K. U individuals care for any member of the species indiscriminately. K individuals care for close kin only. In both cases, the caring behaviour costs the altruist something in terms of his personal survival chances. Suppose we grant Washburn's assumption that U behaviour 'is based on the shared 99 % of genes'. In other words virtually the entire population are universal altruists, and a tiny minority of mutants or immigrants are kin altruists. Superficially, the U gene appears to be caring for copies of itself, since the beneficiaries of its indiscriminate altruism are almost bound to contain the same gene. But is it evolutionarily stable against invasion by initially rare K genes?

No it is not. Every time a rare K individual behaves altruistically, it is especially likely to benefit another K individual *rather than* a U individual. U individuals, on the other hand, give out altruism to K individuals and U individuals indiscriminately, since the defining characteristic of U behaviour is that it is indiscriminate. Therefore K genes are bound to spread through the population at the expense of U genes. Universal altruism is not evolutionarily stable against kin altruism. Even if we assume it to be initially common, it will not remain common. This leads directly into the next, complementary, misunderstanding.

***Misunderstanding 6:
“Kin selection only works for rare genes”***

The logical outcome of the statement that, say, sibling altruism is favoured by natural selection, is that the relevant genes will spread to fixation. Virtually all individuals in the population will be sibling altruists. Therefore, if they did but know it, they would benefit the gene for sibling altruism just as much by caring for a random member of the species as by caring for a sibling! So it might seem that genes for exclusive kin altruism are favoured only when rare.

To put it this way is to expect animals, even genes, to play God. Natural selection is more mechanical than that. The kin altruism gene does not program individuals to take intelligent action on its behalf; it specifies a simple behavioural rule of thumb such as ‘feed squawking gapes in the nest in which you live’. It is this unconscious rule that will become universal when the gene becomes universal.

As in the case of the previous fallacy, we can use the language of evolutionarily stable strategies. We now ask whether kin altruism, K, is stable against invasion by universal altruism, U. That is, we assume that kin altruism has become common and ask whether mutant universal altruist genes will invade. The answer is no, for the same reason as before. The rare universal altruists care for the rival K allele indiscriminately with copies of their own U allele. The K allele, on the contrary, is especially unlikely to care for copies of its rival.

We have shown, therefore, that kin altruism is stable against invasion by universal altruism, but universal altruism is not stable against invasion by kin altruism. This is the nearest I can get to a verbal explanation of Hamilton’s mathematical argument that altruism to close relatives is favoured over universal altruism at all frequencies of the genes concerned. Although it lacks the mathematical precision of Hamilton’s own presentation, it should at least suffice to remove these two common qualitative misunderstandings.

One further point is worth making in connection with these two misunderstandings. Hamilton (1975), in an important paper which deserves more attention, points out that, if a population is divided up into semi-isolated subgroups or ‘towns’, the average relatedness between any two random members of the same town creeps up, because of inbreeding, to a stable value which depends only on the number of inter-town migrants per generation, not on the size of the towns. For instance, if there is one migrant every two generations, the average within-town relatedness climbs to about the level ordinarily expected of full siblings. Hamilton therefore expects sibling-like altruism to prevail between all members of such a semi-isolated town.

This conclusion can be misleading unless carefully qualified. In some ways the high within-town relatedness should be regarded as part of the general background relatedness (equivalent to Hamilton's \bar{r}) rather than as particularly conducive to altruism. Everything turns on what the altruism is being *compared* with. Within a town, as Hamilton agrees, true siblings will be even more closely related to each other than random town members; therefore the behaviour of true siblings should still be altruistic compared with the behaviour of random town members. But, by the same token, random 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; we should expect, Hamilton suggests, strong xenophobia. The point I am making here is that altruism is a relative concept; the behaviour of random fellow town-members towards each other will appear altruistic only by comparison with the xenophobia that is shown to foreigners. Compared with the altruism that is still shown to real siblings, it may appear selfish or indifferent. Fellow town members are, after all, direct competitors for food and other resources. 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).

Misunderstanding 7:

“Altruism is necessarily expected between members of an identical clone”

There are races of parthenogenetic lizards the members of which appear to be identical descendants, in each case, of a single mutant (Maynard Smith 1978). The coefficient of relatedness between individuals within such a clone is 1. A naive application of rote-learned kin selection theory might therefore predict great feats of altruism between all members of the race. Like the previous one, this fallacy is tantamount to a belief that genes are god-like.

Genes for kin-altruism spread because they are especially likely to help copies of themselves rather than of their alleles. But the members of a lizard clone all contain the genes of their original founding matriarch. She was part of an ordinary sexual population, and there is no reason to suppose that she had any special genes for altruism. When she founded her asexual clone, her existing genome was ‘frozen’, a genome that had been shaped by whatever selection pressures had been at work before the clonal mutation.

Should any new mutation for more indiscriminate altruism arise within the clone, the possessors of it would be, by definition, members of a new clone. Evolution could therefore, in theory, now occur by inter-clonal selection. But the new mutation would have to work via a new rule of thumb. If the new rule of thumb is so indiscriminate that both sub-clones benefit, the altruistic sub-clone is bound to decrease, since it is paying the cost of the altruism. We could imagine a new rule of thumb that initially achieved discrimination in favour of the altruistic sub-clone. But this would have to be something like an ordinary ‘close-kin’ altruism rule of thumb, (e.g. ‘care for occupants of your own nest’). Then if the sub-clone possessing this rule of thumb did indeed spread at the expense of the selfish sub-clone, what would we eventually see? Simply a race of lizards each one caring for occupants of her own nest, not clone-wide altruism but ordinary ‘close-kin’ altruism. (Pedants please refrain from commenting that lizards don’t have nests!)

I hasten to add, however, that there are other circumstances in which clonal reproduction is expected to lead to special altruism. Nine-banded armadillos have become a favourite talking point, because they reproduce sexually but each litter consists of four identical quadruplets. Here within-clone altruism is indeed expected, because genes are re-assorted sexually in each generation in the usual way. This means that any gene for clonal altruism is likely to be shared by all members of some clones and no members of rival clones.

There is, so far, no good evidence for or against the predicted within-clone altruism in armadillos. However, some intriguing evidence in a comparable case has been reported by Aoki (1977). In the Japanese aphid *Colophina clematis*, sisterhoods of asexually produced females consist of two types of individuals. Type A females are normal plant-

sucking aphids. Type B females do not progress beyond 1st instar and never reproduce. They have an abnormally short rostrum which is ill-adapted to sucking plants, and enlarged 'pseudoscorpion-like' prothoracic and mesothoracic legs. Aoki showed that Type B females attack large insects and kill them. He speculated that they constitute a sterile 'soldier caste' who protect their reproductive sisters against predators. It is not known how the 'soldiers' feed. Aoki doubts that their fighting mouthparts are capable of absorbing sap. He does not suggest that they are fed by their Type A sisters, but that fascinating possibility is presumably open. He reports indications of similar soldier castes in other aphid genera.

There is a nice irony in Aoki's discussion, brought to my attention by R. L. Trivers. "It may be concluded from [Hamilton's] theory that true sociality should occur more frequently in groups with haplodiploidy than in those without it . . . I do not know how many occurrences of true sociality among animals without haplodiploidy would be sufficient to refute his theory. The existence of soldiers in aphids should take part in one of the gravest problems against his theory, however" (Aoki 1977, P.281).

This error is most instructive. *Colophina clematis*, like other aphids, have winged sexually reproducing dispersal phases interspersed with viviparous parthenogenetic generations. The 'soldiers' and the Type A individuals whom they seem to protect are wingless, and are almost certainly members of the same clone. The regular intervention of winged sexual generations ensures that genes for facultatively developing into a soldier, and alleles for not doing so, would be shuffled throughout the population. Some clones would therefore have such genes while rival clones would not. Conditions, in fact, are quite different from those of the lizards, and are ideal for the evolution of sterile castes. The soldiers and their reproductive clone mates are best regarded as parts of the same extended body (Janzen 1977). If a soldier aphid altruistically sacrifices her own reproduction, then so does my big toe. In almost exactly the same sense!

Misunderstanding 8:

“Sterile worker insects propagate their genes by caring for other sterile workers who are especially closely related to them”

Barash, referring to Trivers and Hare's (1976) elaboration of Hamilton's well known haplodiploidy theory, says: “. . . important support has been provided for Hamilton's theory by the demonstration that workers provide three times the food for their sisters (other workers) as they do for their brothers (the drones), consistent with their three-fourths versus one fourth genetic relationship” (Barash 1977, p. 84).

In fact, Trivers and Hare were most emphatically not concerned with how much food workers gave to other workers. The whole point of their paper was the relative investment in male and female *reproductives*. They predicted three times as much investment by workers in young *queens* as in drones; investment in other sterile workers did not come into the picture. This error has previously been criticised by Krebs (1977).

To make the general point, it is an error to predict altruism between individuals simply because they share genes. For an altruistic gene to spread, it is necessary that the beneficiary of the altruism should propagate it; ultimately she must do some reproducing! Workers care for other workers, only so that those other workers can ultimately benefit reproductives. It is irrelevant how many genes workers share with each other; what is relevant is how many genes workers share with the reproductives who are ultimately cared for.

A good way of thinking about these matters is to regard each would-be beneficiary of an altruistic act as a machine for producing children of a certain kind. From my point of view, my daughter is a grandchild-producing machine; my sister is a niece/nephew-producing machine, but *not* if she is a sterile worker!

Incidentally, this way of thinking leads to an interesting general point. If my mother is guaranteed monogamous, or was fertilised for life by my father only, she is a full sibling-producing machine. I myself am potentially an offspring-producing machine. Full siblings and offspring are equally valuable to me. Therefore my mother, under these conditions, is exactly as valuable to me as I am myself, or as my identical twin would be. We should therefore not be surprised to find tendencies toward eusociality in any groups where females store sperm from one male for life or are reliably monogamous. But there is a danger in this line of reasoning, which is the subject of the next section.

Misunderstanding 9:

“Because full siblings are no less valuable to an individual than his own offspring, Trivers’s theory of parent/offspring conflict does not apply to monogamous species”

Consider Trivers’s (1974) well known theory of parent/offspring conflict. In the light of the preceding section, a critic might be tempted to say that in monogamous species, in which siblings can count on being full siblings, Trivers is wrong to expect parent/offspring conflict. The reasoning is as follows. It is all very well for Trivers to say that an individual is twice as closely related to himself as he is to any sibling, but the individual is only ‘valuable’ as an offspring-making machine. His potential future offspring are no closer to himself than his siblings are. Therefore he should be just as happy to see his siblings fed as himself, and Trivers’s basic reason for expecting parent-offspring conflict vanishes. Our critic claims that Trivers’s conclusions are right only in polygamous species in which siblings can count on being half siblings.

The critic’s error is an appealing one, and it is genuinely difficult to refute it. In effect, what he is doing is applying the ‘reproducing-machine’ formula inconsistently: he is applying it to the individual himself, but not to the sibling. He is effectively claiming that the relevant comparison “is not between Ego’s r with his sib and his r with himself, but is between Ego’s r with his own offspring and his r with his sib” (Hartung 1977). But, to be consistent, we *should* either compare Ego with his sib, or Ego’s offspring with his sib’s offspring; in either case Trivers would then turn out to be right.

Consider it another way. The mother has a pint of milk which she ‘wishes’ to divide equally among her two children. Trivers expects each child to try to grab more than half a pint, hence he expects conflict between each child and the mother. Our critic expects each child to be content with half a pint, because each child sees his full sib as equivalent to one of his own potential offspring. But the choice that is actually open is over who is going to get the milk. There is no question of Ego’s *child* getting the milk, for he does not yet exist; the contenders are himself and his sib, i. e. a niece/nephew-making machine ($r = 1/4$) versus an offspring-making machine ($r = 1/2$). If Ego’s choice were over whether to give milk to his own offspring or to a full sib of exactly the same age and circumstances as his own offspring, then the critic would be right: Ego would be indifferent. But this is not the choice that exists. When the two practical contenders for the milk are Ego and his sib, Trivers is right to predict conflict.

I frequently encounter this error in conversation, but have not seen it spelled out in print. Hartung (1977) reaches the same conclusion as my anonymous critic, but by a different route which is not entirely clear to me, and I am not sure whether his reasoning is subject to some more sophisticated version of my objection, or whether he has identified some

special conditions under which we should truly not expect parent/offspring conflict.

Misunderstanding 10:

“Individuals should tend to inbreed, simply because this brings extra close relatives into the world”

I have to be careful here, because there is a correct line of reasoning that sounds very like the error. Moreover there may be other selection pressures for and against inbreeding, but these have nothing to do with the present argument: the proponent of the misconception is assumed to have covered himself with an ‘other things being equal’.

The reasoning I wish to criticize runs as follows. Assume a monogamous mating system. A female who mates with a random male brings into the world a child related to her by $r = 1/2$. If only she had mated with her brother she would have brought into the world a ‘super-child’ with an effective coefficient of relatedness of $3/4$ (Hamilton 1972). Therefore genes for inbreeding are propagated at the expense of genes for outbreeding, having a greater probability of getting into each child born.

The error is a simple one. If the individual refrains from mating with her brother, he is free to mate with some other female. So an outbreeding female gains a nephew/niece ($r = 1/4$) plus a normal child of her own ($r = 1/2$) to match the single super-child of the incestuous female (effective $r = 3/4$).

It is important to note that the refutation of the error assumes the equivalent of monogamy. If the species is, say, polygynous with high variance in male reproductive success and a large bachelor population, things can be very different (Maynard Smith 1978; Parker 1979). It is now no longer true that a female, by mating with her brother, deprives him of the chance to mate with someone else. Most probably, the free mating his sister gives him is the only mating he will get. The female therefore does not deprive herself of an independent niece/nephew by mating incestuously, and she does bring into the world a child who is a super-child from her own genetic point of view. There may, then, be selection pressures in favour of incest, but the heading to this section is, as a general statement, incorrect.

Misunderstanding 11:

“There is an important distinction between exact and probabilistic coefficients of relatedness which affects the kind of altruistic behaviour predicted”

The coefficient of relatedness, r , can mean one of two things, which are usually quantitatively equal. It can mean the *probability* that a gene in one individual will be identical by descent to one in a given relative. Or it can mean the *proportion* of one individual's genome that is identical by descent with the relative's genome.

Barash et al. (1978) make much of the distinction between ‘Exact versus probabilistic coefficients of relationship’. If you think of r as a proportion rather than a probability, it is true that it is a deterministically fixed quantity for the parent/child relationship but a probabilistic average for all other relationships. Thus *on average* two brothers will share 50% of their genes (identical by descent), but for any given pair of brothers the true figure could be more or it could be less. But this exact/probabilistic dichotomy is simply a consequence of the proportion way of thinking about r . The *probability* that a gene in a father will be inherited by his son is (by definition) not a deterministic figure, it is an average one (Dawkins 1976b, 1978).

The only reason it is worth criticising this otherwise innocuously pointless way of thinking is that it can lead to outright error, as Partridge and Nunney (1977) have pointed out in a critique of Fagen (1976). As another example, Barash et al. suggest that selection might favour:

“a degree of discrimination among siblings not found between parent and offspring. This discrimination could derive from the selective advantage accruing to individuals who recognize their relatedness to others and behave altruistically in direct proportion to r . By contrast, such discrimination would not in itself be adaptive for parent-infant dyads, since all offspring are of exactly equal genetic relatedness . . . Relative phenotypic similarity between any two siblings should generally correlate with the magnitude of their shared r . . .”

In other words individuals are expected to try to pick out those of their siblings who resemble them for special altruistic treatment.

The error is immediately apparent when we switch from proportion language to probability language. If I want to guess whether your hand of cards contains the ace of spades I would be quite wrong to say: I already know you have the 2, 3, 5, 6, 7, 9, 10, Jack and King of spades; therefore you have a strong hand in spades; therefore you probably have the ace! Similarly, there is no particular reason to suppose that a brother

who has my hair colour, eye colour, nose shape and musical ability therefore probably has my gene for brotherly altruism. Unless, of course, we allow for genetic linkage or pleiotropy, but this brings us right back to the main point of this section.

Barash et al. seem to be partially aware of the theoretical danger they are in, because they try to cover themselves. They preface their remarks by assuming “pleiotropy and a positive correlation between the phenotypic resemblance of any two individuals and their shared r . . .” But although this renders part of their statement quoted above technically correct, it unfortunately also undermines the whole point of their paper. For if we are allowed to assume pleiotropy or linkage between genes for recognition-features and genes for altruism, Barash et al.’s point applies to the parent/child relationship every bit as strongly as to the sibling relationship. No matter how we play it, we cannot find a set of assumptions that predicts a separation between the ‘exact’ parent/child relationship and the ‘probabilistic’ sibling relationship. The distinction between exact and probabilistic coefficients of relationship has yet to be shown to have any importance at all. I should confess at this point that I am one of those who has emphasised it (Dawkins 1976a, p. 98) although I did not actually draw any erroneous conclusions from it. I did, however, categorically state the next error.

Misunderstanding 12:

“An animal is expected to dole out to each relative an amount of altruism proportional to the coefficient of relatedness”

As Altmann (1979) has pointed out, I perpetrated this error when I wrote that “second cousins should tend to receive 1/16 as much altruism as offspring or siblings (Dawkins 1976 a). To oversimplify Altmann’s argument, suppose I have a cake that I am going to give to my relatives, how should I divide it? The fallacy under discussion amounts to cutting the cake in such a way that each relative gets a slice whose size is proportional to his coefficient of relatedness to me. Really, of course there is better reason to give the entire cake to the closest relative available and none to any of the others

Suppose each mouthful of cake was equally valuable, translated into offspring flesh in simple pro-rata fashion. Then clearly an individual should prefer that his whole cake should be translated into closely related flesh than distantly related flesh. Of course this simple pro-rata assumption would almost certainly be false in real cases. However, quite elaborate assumptions about diminishing returns would have to be made before we could sensibly predict that the cake should be divided in exact proportion to coefficients of relatedness. Therefore, although my statement quoted above could under special circumstances be true, as a generalisation it is properly regarded as fallacious. Of course I didn’t really *mean* it anyway!

Apology

If the foregoing pages seem destructive or negative in tone, the very opposite was my intention. The art of explaining difficult material consists, in part, of anticipating the reader's difficulties and forestalling them. Systematically exposing common misunderstandings can therefore be a positively constructive exercise. I believe I understand kin selection better for having met these twelve errors, for having, in many cases, fallen into the trap myself and struggled painfully out the other side.

Summary

Hamilton's theory of kin selection now sometimes provokes the scepticism that any bandwagon may deserve, but in this case most of the problems are due to misunderstanding. This paper uses non-mathematical language to refute the following 12 common errors: "kin selection is a special, complex kind of natural selection"; "kin selection is a form of group selection"; "kin selection requires formidable feats of cognitive reasoning by animals"; "it is hard to imagine a gene 'for' altruistic behaviour"; "all species members share the majority of their genes, so selection should favour universal altruism"; "kin selection only works for rare genes"; "altruism is necessarily expected between members of an identical clone"; "sterile workers care for other workers because they are close relatives"; "Trivers's theory of parent/offspring conflict does not apply to monogamous species"; "individuals should tend to inbreed, simply because that brings close relatives into the world"; "when relatedness is probabilistic rather than exact, altruists will favour relatives of a given type who especially resemble them"; "animals are expected to dole out to each relative an amount of altruism proportional to the coefficient of relatedness". The exposing of common

errors is a constructive, not a destructive exercise.

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