

## CHAPTER 6

### Genesmanship

p. 90 . . . *I have never been able to understand why they have been so neglected . . .*

Hamilton's 1964 papers are neglected no longer. The history of their earlier neglect and subsequent recognition makes an interesting quantitative study in its own right, a case study in the incorporation of a 'meme' into the meme pool. I trace the progress of this meme in the notes to Chapter 11.

p. 90 . . . *I shall assume that we are talking about genes that are rare . . .*

The device of assuming that we are talking about a gene that is rare in the population as a whole was a bit of a cheat, to make the measuring of relatedness easy to explain. One of Hamilton's main achievements was to show that his conclusions follow *regardless* of whether the gene concerned is rare or common. This turns out to be an aspect of the theory that people find difficult to understand.

The problem of measuring relatedness trips many of us up in the following way. Any two members of a species, whether they belong to the same family or not, usually share more than 90 per cent of their genes. What, then, are we talking about when we speak of the relatedness between brothers as  $\frac{1}{2}$ , or between first cousins as  $\frac{1}{4}$ ? The answer is that brothers share  $\frac{1}{2}$  of their genes *over and above* the 90 per cent (or whatever it is) that all individuals share in any case. There is a kind of baseline relatedness, shared by all members of a species; indeed, to a lesser extent, shared by members of other species. Altruism is expected towards individuals whose relatedness is higher than the baseline, whatever the baseline happens to be.

In the first edition, I evaded the problem by using the trick of talking about rare genes. This is correct as far as it goes, but it doesn't go far enough. Hamilton himself wrote of genes being 'identical by descent', but this presents difficulties of its own, as Alan Grafen has shown. Other writers did not even acknowledge that there was a problem, and simply spoke of absolute percentages of shared genes, which is a definite and positive error. Such careless talk did lead to serious misunderstandings. For instance a distinguished anthropologist, in the course of a bitter attack on 'sociobiology' published in 1978, tried to argue that if we took kin selection seriously we should expect all humans to be altruistic to one another, since all humans share more than 99 per cent of their genes. I have given a brief reply to this error in my 'Twelve Misunderstandings of Kin Selection' (it rates as

Misunderstanding Number 5). The other eleven misunderstandings are worth a look, too.

Alan Grafen gives what may be the definitive solution to the problem of measuring relatedness in his 'Geometric View of Relatedness', which I shall not attempt to expound here. And in another paper, 'Natural Selection, Kin Selection and Group Selection', Grafen clears up a further common and important problem, namely the widespread misuse of Hamilton's concept of 'inclusive fitness'. He also tells us the right and wrong way to calculate costs and benefits to genetic relatives.

p. 93 . . . *armadillos . . . it would be well worth somebody's while going out to South America to have a look.*

No developments are reported on the armadillo front, but some spectacular new facts have come to light for another group of 'cloning' animals—aphids. It has long been known that aphids (e.g. greenfly) reproduce asexually as well as sexually. If you see a crowd of aphids on a plant, the chances are that they are all members of an identical female clone, while those on the next-door plant will be members of a different clone. Theoretically these conditions are ideal for the evolution of kin-selected altruism. No actual instances of aphid altruism were known, however, until sterile 'soldiers' were discovered in a Japanese species of aphids by Shigeyuki Aoki, in 1977, just too late to appear in the first edition of this book. Aoki has since found the phenomenon in a number of different species, and has good evidence that it has evolved at least four times independently in different groups of aphids.

Briefly, Aoki's story is this. Aphid 'soldiers' are an anatomically distinct caste, just as distinct as the castes of traditional social insects like ants. They are larvae that do not mature to full adulthood, and they are therefore sterile. They neither look nor behave like their non-soldier larval contemporaries, to whom they are, however, *genetically* identical. Soldiers are typically larger than non-soldiers; they have extra-big front legs which make them look almost scorpion-like; and they have sharp horns pointing forward from the head. They use these weapons to fight and kill would-be predators. They often die in the process, but even if they don't it is still correct to think of them as genetically 'altruistic' because they are sterile.

In terms of selfish genes, what is going on here? Aoki does not mention precisely what determines which individuals become sterile soldiers and which become normal reproductive adults, but we can safely say that it must be an environmental, not a genetic difference—obviously, since the sterile soldiers and the normal aphids on any one plant are genetically identical. However, there must be genes for the capacity to be environmentally switched into either of the two developmental pathways. Why has natural selection favoured these genes, even though some of them end up in the

bodies of sterile soldiers and are therefore not passed on? Because, thanks to the soldiers, copies of those very same genes have been saved in the bodies of the reproductive non-soldiers. The rationale is just the same as for all social insects (see Chapter 10), except that in other social insects, such as ants or termites, the genes in the sterile 'altruists' have only a *statistical* chance of helping copies of themselves in non-sterile reproductives. Aphid altruistic genes enjoy certainty rather than statistical likelihood since aphid soldiers are clone-mates of the reproductive sisters whom they benefit. In some respects Aoki's aphids provide the neatest real-life illustration of the power of Hamilton's ideas.

Should aphids, then, be admitted to the exclusive club of truly social insects, traditionally the bastion of ants, bees, wasps and termites? Entomological conservatives could blackball them on various grounds. They lack a long-lived old queen, for instance. Moreover, being a true clone, the aphids are no more 'social' than the cells of your body. There is a single animal feeding on the plant. It just happens to have its body divided up into physically separate aphids, some of which play a specialized defensive role just like white blood corpuscles in the human body. 'True' social insects, the argument goes, cooperate in spite of not being part of the same organism, whereas Aoki's aphids cooperate because they do belong to the same 'organism'. I cannot get worked up about this semantic issue. It seems to me that, so long as you understand what is going on among ants, aphids and human cells, you should be at liberty to call them social or not, as you please. As for my own preference, I have reasons for calling Aoki's aphids social organisms, rather than parts of a single organism. There are crucial properties of a single organism which a single aphid possesses, but which a clone of aphids does not possess. The argument is spelled out in *The Extended Phenotype*, in the chapter called 'Rediscovering the Organism', and also in the new chapter of the present book called 'The Long Reach of the Gene'.

p. 94 *Kin selection is emphatically not a special case of group selection.*

The confusion over the difference between group selection and kin selection has not disappeared. It may even have got worse. My remarks stand with redoubled emphasis except that, by a thoughtless choice of words, I introduced a quite separate fallacy of my own at the top of page 102 of the first edition of this book. I said in the original (it is one of the few things I have altered in the text of this edition): 'We simply expect that second cousins should tend to receive  $\frac{1}{8}$  as much altruism as offspring or siblings.' As S. Altmann has pointed out, this is obviously wrong. It is wrong for a reason that has nothing to do with the point I was trying to argue at the time. If an altruistic animal has a cake to give to relatives, there is no reason at all for it to give every relative a slice, the size of the slices being determined

by the closeness of relatedness. Indeed, this would lead to absurdity since all members of the species, not to mention other species, are at least distant relatives who could therefore each claim a carefully measured crumb! On the contrary, if there is a close relative in the vicinity, there is no reason to give a distant relative any cake at all. Subject to other complications like laws of diminishing returns, the whole cake should be given to the closest relative available. What I of course meant to say was 'We simply expect that second cousins should be  $\frac{1}{8}$  as likely to receive altruism as offspring or siblings' (p. 94), and this is what now stands.

p. 94 *He deliberately excludes offspring: they don't count as kin!*

I expressed the hope that E. O. Wilson would change his definition of kin selection in future writings, so as to include offspring as 'kin'. I am happy to report that, in his *On Human Nature*, the offending phrase, 'other than offspring', has indeed—I am not claiming any credit for this!—been omitted. He adds, '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.' This is unfortunately an accurate statement about ordinary usage by biologists, which simply reflects the fact that many biologists still lack a gut understanding of what kin selection is fundamentally all about. They *still* wrongly think of it as something extra and esoteric, over and above ordinary 'individual selection'. It isn't. Kin selection follows from the fundamental assumptions of neo-Darwinism as night follows day.

p. 96 *But what a complicated calculation . . .*

The fallacy that the theory of kin selection demands unrealistic feats of calculation by animals is revived without abatement by successive generations of students. Not just young students, either. *The Use and Abuse of Biology*, by the distinguished social anthropologist Marshall Sahlins, could be left in decent obscurity had it not been hailed as a 'withering attack' on 'sociobiology'. The following quotation, in the context of whether kin selection could work in humans, is almost too good to be true:

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] =  $\frac{1}{8}$ .

This is not the first time I have quoted this highly revealing passage, and I may as well quote my own rather uncharitable reply to it, from 'Twelve Misunderstandings of Kin Selection':

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  $m$ , the coefficient of refraction? How do green plants 'figure out' the formula of chlorophyll?

The fact is that if you thought about anatomy, physiology, or almost any aspect of biology, not just behaviour, in Sahlins's way you would arrive at his same non-existent problem. The embryological development of any bit of an animal's or plant's body requires complicated mathematics for its complete description, but this does not mean that the animal or plant must itself be a clever mathematician! Very tall trees usually have huge buttresses flaring out like wings from the base of their trunks. Within any one species, the taller the tree, the relatively larger the buttresses. It is widely accepted that the shape and size of these buttresses are close to the economic optimum for keeping the tree erect, although an engineer would require quite sophisticated mathematics to demonstrate this. It would never occur to Sahlins or anyone else to doubt the theory underlying buttresses simply on the grounds that trees lack the mathematical expertise to do the calculations. Why, then, raise the problem for the special case of kin selected behaviour? It can't be because it is behaviour as opposed to anatomy, because there are plenty of other examples of behaviour (other than kin-selected behaviour, I mean) that Sahlins would cheerfully accept without raising his 'epistemological' objection; think, for instance, of my own illustration (p. 96) of the complicated calculations that in some sense we all must do whenever we catch a ball. One cannot help wondering: are there social scientists who are quite happy with the theory of natural selection generally but who, for quite extraneous reasons that may have roots in the history of their subject, desperately want to find something—*anything*—wrong with the theory of *kin selection specifically*?

p. 99 . . . *we have to think how animals might actually go about estimating who their close relations are . . . We know who our relations are because we are told . . .*

The whole subject of kin recognition has taken off in a big way since this book was written. Animals, including ourselves, seem to show remarkably subtle abilities to discriminate relatives from nonrelatives, often by smell. A recent book, *Kin Recognition in Animals*, summarizes what is now known. The chapter on humans by Pamela Wells shows that the statement above ('We know who our relations are because we are told') needs to be supplemented: there is at least circumstantial evidence that we are capable of using various nonverbal cues, including the smell of our relatives' sweat. The whole subject is, for me, epitomized by the quotation with which she begins:

all good kumrads you can tell  
by their altruistic smell

e. e. cummings

Relatives might need to recognize one another for reasons other than altruism. They might also want to strike a balance between outbreeding and inbreeding, as we shall see in the next note.

p. 99 . . . *the injurious effects of recessive genes which appear with inbreeding. (For some reason many anthropologists do not like this explanation.)*

A lethal gene is one that kills its possessor. A recessive lethal, like any recessive gene, doesn't exert its effect unless it is in double dose. Recessive lethals get by in the gene pool, because most individuals possessing them have only one copy and therefore never suffer the effects. Any given lethal is rare, because if it ever gets common it meets copies of itself and kills off its carriers. There could nevertheless be lots of different types of lethal, so we could still all be riddled with them. Estimates vary as to how many different ones there are lurking in the human gene pool. Some books reckon as many as two lethals, on average, per person. If a random male mates with a random female, the chances are that his lethals will not match hers and their children will not suffer. But if a brother mates with a sister, or a father with a daughter, things are ominously different. However rare my lethal recessives may be in the population at large, and however rare my sister's lethal recessives may be in the population at large, there is a disquietingly high chance that hers and mine are the same. If you do the sums, it turns out that, for every lethal recessive that I possess, if I mate with my sister one in eight of our offspring will be born dead or will die young. Incidentally, dying in adolescence is even more 'lethal', genetically speaking, than dying at birth: a stillborn child doesn't waste so much of the parents' vital time and

energy. But, whichever way you look at it, close incest is not just mildly deleterious. It is potentially catastrophic. Selection for active incest-avoidance could be as strong as any selection pressure that has been measured in nature.

Anthropologists who object to Darwinian explanations of incest-avoidance perhaps do not realize what a strong Darwinian case they are opposing. Their arguments are sometimes so weak as to suggest desperate special pleading. They commonly say, for instance: 'If Darwinian selection had really built into us an instinctive revulsion against incest, we wouldn't need to forbid it. The taboo only grows up because people have incestuous lusts. So the rule against incest cannot have a "biological" function, it must be purely "social".' This objection is rather like the following: 'Cars don't need locks on the ignition switch because they have locks on the doors. Therefore ignition locks cannot be anti-theft devices; they must have some purely ritual significance!' Anthropologists are also fond of stressing that different cultures have different taboos, indeed different definitions of kinship. They seem to think that this, too, undermines Darwinian aspirations to explain incest-avoidance. But one might as well say that sexual desire cannot be a Darwinian adaptation because different cultures prefer to copulate in different positions. It seems to me highly plausible that incest-avoidance in humans, no less than in other animals, is the consequence of strong Darwinian selection.

Not only is it a bad thing to mate with those genetically too close to you. Too-distant outbreeding can also be bad because of genetic incompatibilities between different strains. Exactly where the ideal intermediate falls is not easy to predict. Should you mate with your first cousin? With your second or third cousin? Patrick Bateson has tried to ask Japanese quail where their own preferences lie along the spectrum. In an experimental set-up called the Amsterdam Apparatus, birds were invited to choose among members of the opposite sex arrayed behind miniature shop-windows. They preferred first cousins over both full siblings and unrelated birds. Further experiments suggested that young quail learn the attributes of their clutch-companions, and then, later in life, tend to choose sexual partners that are quite like their clutch-mates but not too like them.

Quail, then, seem to avoid incest by their own internal lack of desire for those with whom they have grown up. Other animals do it by observing social laws, socially imposed rules of dispersal. Adolescent male lions, for instance, are driven out of the parental pride where female relatives remain to tempt them, and breed only if they manage to usurp another pride. In chimpanzee and gorilla societies it tends to be the young females who leave to seek mates in other bands. Both dispersal patterns, as well as the quail's system, are to be found among the various cultures of our own species.

p. 103 *Since [cuckoo hosts] are not in danger of being parasitized by members of their own species . . .*

This is probably true of most species of birds. Nevertheless, we should not be surprised to find some birds parasitizing nests of their own species. And the phenomenon is, indeed, being found in an increasing number of species. This is especially so now that new molecular techniques are coming in for establishing who is related to whom. Actually, the selfish gene theory might expect it to happen even more often than we so far know.

p. 105 *Kin selection in lions*

Bertram's emphasis on kin selection as the prime mover of cooperation in lions has been challenged by C. Packer and A. Pusey. They claim that in many prides the two male lions are not related. Packer and Pusey suggest that reciprocal altruism is at least as likely as kin selection as an explanation for cooperation in lions. Probably both sides are right. Chapter 12 emphasizes that reciprocation ('Tit for Tat') can evolve only if a critical quorum of reciprocators can initially be mustered. This ensures that a would-be partner has a decent chance of being a reciprocator. Kinship is perhaps the most obvious way for this to happen. Relatives naturally tend to resemble one another, so even if the critical frequency is not met in the population at large it may be met within the family. Perhaps cooperation in lions got its start through the kin-effects suggested by Bertram, and this provided the necessary conditions for reciprocation to be favoured. The disagreement over lions can be settled only by facts, and facts, as ever, tell us only about the particular case, not the general theoretical argument.

p. 105 *If C is my identical twin . . .*

It is now widely understood that an identical twin is theoretically as valuable to you as you are to yourself—as long as the twin really is guaranteed identical. What is not so widely understood is that the same is true of a guaranteed monogamous mother. If you know for certain that your mother will continue to produce your father's children and only your father's children, your mother is as genetically valuable to you as an identical twin, or as yourself. Think of yourself as an offspring-producing machine. Then your monogamous mother is a (full) sibling-producing machine, and full siblings are as genetically valuable to you as your own offspring. Of course this neglects all kinds of practical considerations. For instance, your mother is older than you, though whether this makes her a better or worse bet for future reproduction than you yourself depends on particular circumstances—we can't give a general rule.

That argument assumes that your mother can be relied upon to continue producing your father's children, as opposed to some other male's children.

The extent to which she can be relied upon depends upon the mating system of the species. If you are a member of a habitually promiscuous species, you obviously cannot count on your mother's offspring being your full siblings. Even under ideally monogamous conditions, there is one apparently inescapable consideration that tends to make your mother a worse bet than you are yourself. You father may die. With the best will in the world, if your father is dead your mother can hardly be expected to go on producing his children, can she?

Well, as a matter of fact she can. The circumstances under which this can happen are obviously of great interest for the theory of kin selection. As mammals we are used to the idea that birth follows copulation after a fixed and rather short interval. A human male can father young posthumously, but not after he has been dead longer than nine months (except with the aid of deep-freezing in a sperm-bank). But there are several groups of insects in which a female stores sperm inside herself for the whole of her life, eking it out to fertilize eggs as the years go by, often long years after the death of her mate. If you are a member of a species that does this, you can potentially be really very sure that your mother will continue to be a good 'genetic bet'. A female ant mates only in a single mating flight, early in her life. The female then loses her wings and never mates again. Admittedly, in many ant species the female mates with several males on her mating flight. But if you happen to belong to one of those species whose females are always monogamous, you really can regard your mother as at least as good a genetic bet as you are yourself. The great point about being a young ant, as opposed to a young mammal, is that it doesn't matter whether your father is dead (indeed, he almost certainly *is* dead!). You can be pretty sure that your father's sperm are living on after him, and that your mother can continue to make full siblings for you.

It follows that, if we are interested in the evolutionary origins of sibling care and of phenomena like the insect soldiers, we should look with special attention towards those species in which females store sperm for life. In the case of ants, bees, and wasps there is, as Chapter 10 discusses, a special genetic peculiarity—haplodiploidy—that may have predisposed them to become highly social. What I am arguing here is that haplodiploidy is not the only predisposing factor. The habit of lifetime sperm-storage may have been at least as important. Under ideal conditions it can make a mother as genetically valuable, and as worthy of 'altruistic' help, as an identical twin.

p. 106 . . . *social anthropologists might have interesting things to say.* This remark now makes me blush with embarrassment. I have since learned that social anthropologists not only have things to say about the 'mother's brother effect': many of them have for years spoken of little else! The effect that I 'predicted' is an empirical fact in a large number of cultures that has

been well known to anthropologists for decades. Moreover, when I suggested the specific hypothesis that 'in a society with a high degree of marital infidelity, maternal uncles should be more altruistic than "fathers", since they have more grounds for confidence in their relatedness to the child' (p. 106), I regrettably overlooked the fact that Richard Alexander had already made the same suggestion (a footnote acknowledging this was inserted in later printings of the first edition of this book). The hypothesis has been tested, by Alexander himself among others, using quantitative counts from the anthropological literature, with favourable results.

## CHAPTER 7

### Family planning

p. 110 *Wynne-Edwards . . . has been mainly responsible for promulgating the idea of group selection.*

Wynne-Edwards is generally treated more kindly than academic heretics often are. By being wrong in an unequivocal way, he is widely credited (though I personally think this point is rather overdone) with having provoked people into thinking more clearly about selection. He himself made a magnanimous recantation in 1978, when he wrote:

The general consensus of theoretical biologists at present is that credible models cannot be devised, by which the slow march of group selection could overtake the much faster spread of selfish genes that bring gains in individual fitness. I therefore accept their opinion.

Magnanimous these second thoughts may have been, but unfortunately he has had third ones: his latest book re-recants.

Group selection, in the sense in which we have all long understood it, is even more out of favour among biologists than it was when my first edition was published. You could be forgiven for thinking the opposite: a generation has grown up, especially in America, that scatters the name 'group selection' around like confetti. It is littered over all kinds of cases that used to be (and by the rest of us still are) clearly and straightforwardly understood as something else, say kin selection. I suppose it is futile to become too annoyed by such semantic parvenus. Nevertheless, the whole issue of group selection was very satisfactorily settled a decade ago by John Maynard Smith and others, and it is irritating to find that we are now two generations, as well as two nations, divided only by a common language. It is particularly unfortunate that philosophers, now belatedly entering the field, have started out muddled by this recent caprice of terminology. I recommend Alan