6

Genesmanship

What is the selfish gene? It is not just one single physical bit of DNA. Just as in the primeval soup, it is *all replicas* of a particular bit of DNA, distributed throughout the world. If we allow ourselves the licence of talking about genes as if they had conscious aims, always reassuring ourselves that we could translate our sloppy language back into respectable terms if we wanted to, we can ask the question, what is a single selfish gene trying to do? It is trying to get more numerous in the gene pool. Basically it does this by helping to program the bodies in which it finds itself to survive and to reproduce. But now we are emphasizing that 'it' is a distributed agency, existing in many different individuals at once. The key point of this chapter is that a gene might be able to assist *replicas* of itself that are sitting in other bodies. If so, this would appear as individual altruism but it would be brought about by gene selfishness.

Consider the gene for being an albino in man. In fact several genes exist that can give rise to albinism, but I am talking about just one of them. It is recessive; that is, it has to be present in double dose in order for the person to be an albino. This is true of about 1 in 20,000 of us. But it is also present, in single dose, in about 1 in 70 of us, and these individuals are not albinos. Since it is distributed in many individuals, a gene such as the albino gene could, in theory, assist its own survival in the gene pool by programming its bodies to behave altruistically towards other albino bodies, since these are known to contain the same gene. The albino gene should be quite happy if some of the bodies that it inhabits die, provided that in doing so they help other bodies containing the same gene to survive. If the albino gene could make one of its bodies save the lives of ten albino bodies, then even the death of the altruist is amply compensated by the increased numbers of albino genes in the gene pool.

Should we then expect albinos to be especially nice to each other? Actually the answer is probably no. In order to see why not, we must

temporarily abandon our metaphor of the gene as a conscious agent, because in this context it becomes positively misleading. We must translate back into respectable, if more longwinded terms. Albino genes do not really 'want' to survive or to help other albino genes. But if the albino gene just happened to cause its bodies to behave altruistically towards other albinos, then automatically, willy-nilly, it would tend to become more numerous in the gene pool as a result. But, in order for this to happen, the gene would have to have two independent effects on bodies. Not only must it confer its usual effect of a very pale complexion. It must also confer a tendency to be selectively altruistic towards individuals with a very pale complexion. Such a double-effect gene could, if it existed, be very successful in the population.

Now it is true that genes do have multiple effects, as I emphasized in Chapter 3. It is theoretically possible that a gene could arise which conferred an externally visible 'label', say a pale skin, or a green beard, or anything conspicuous, and also a tendency to be specially nice to bearers of that conspicuous label. It is possible, but not particularly likely. Green beardedness is just as likely to be linked to a tendency to develop ingrowing toenails or any other trait, and a fondness for green beards is just as likely to go together with an inability to smell freesias. It is not very probable that one and the same gene would produce both the right label and the right sort of altruism. Nevertheless, what may be called the Green Beard Altruism Effect is a theoretical possibility.

An arbitrary label like a green beard is just one way in which a gene might 'recognize' copies of itself in other individuals. Are there any other ways? A particularly direct possible way is the following. The possessor of an altruistic gene might be recognized simply by the fact that he does altruistic acts. A gene could prosper in the gene pool if it 'said' the equivalent of: 'Body, if *A* is drowning as a result of trying to save someone else from drowning, jump in and rescue *A*.' The reason such a gene could do well is that there is a greater than average chance that *A* contains the same life-saving altruistic gene. The fact that *A* is seen to be trying to rescue somebody else is a label, equivalent to a green beard. It is less arbitrary than a green beard, but it still seems rather implausible. Are there any plausible ways in which genes might 'recognize' their copies in other individuals?

The answer is yes. It is easy to show that *close relatives*—kin—have a greater than average chance of sharing genes. It has long been clear that this must be why altruism by parents towards their young is so common. What R. A. Fisher, J. B. S. Haldane, and especially W. D. Hamilton realized, was that the same applies to other close relations—brothers and sisters, nephews and nieces, close cousins. If an individual dies in order to save ten close relatives, one copy of the kin-altruism gene may be lost, but a larger number of copies of the same gene is saved.

'A larger number' is a bit vague. So is 'close relatives'. We can do better than that, as Hamilton showed. His two papers of 1964 are among the most important contributions to social ethology ever written, and I have never been able to understand why they have been so neglected by ethologists (his name does not even appear in the index of two major text-books of ethology, both published in 1970).* Fortunately there are recent signs of a revival of interest in his ideas. Hamilton's papers are rather mathematical, but it is easy to grasp the basic principles intuitively, without rigorous mathematics, though at the cost of some over-simplification. The thing we want to calculate is the probability, or odds, that two individuals, say two sisters, share a particular gene.

For simplicity I shall assume that we are talking about genes that are rare in the gene pool as a whole.* Most people share 'the gene for not being an albino', whether they are related to each other or not. The reason this gene is so common is that in nature albinos are less likely to survive than non-albinos because, for example, the sun dazzles them and makes them relatively unlikely to see an approaching predator. We are not concerned with explaining the prevalence in the gene pool of such obviously 'good' genes as the gene for not being an albino. We are interested in explaining the success of genes specifically as a result of their altruism. We can therefore assume that, at least in the early stages of this process of evolution, these genes are rare. Now the important point is that even a gene that is rare in the population as a whole is common within a family. I contain a number of genes that are rare in the population as a whole, and you also contain genes that are rare in the population as a whole. The chance that we both contain the same rare genes is very small indeed. But the chances are good that my sister contains a particular rare gene that I contain, and the chances are equally good that your sister contains a rare gene in common with you. The odds are in this case exactly 50 per cent, and it is easy to explain why.

Suppose you contain one copy of the gene *G*. You must have

received it either from your father or from your mother (for convenience we can neglect various infrequent possibilities—that *G* is a new mutation, that both your parents had it, or that either of your parents had two copies of it). Suppose it was your father who gave you the gene. Then every one of his ordinary body cells contained one copy of *G*. Now you will remember that when a man makes a sperm he doles out half his genes to it. There is therefore a 50 per cent chance that the sperm that begot your sister received the gene *G*. If, on the other hand, you received *G* from your mother, exactly parallel reasoning shows that half of her eggs must have contained *G*; once again, the chances are 50 per cent that your sister contains *G*. This means that if you had 100 brothers and sisters, approximately 50 of them would contain any particular rare gene that you contain. It also means that if you have 100 rare genes, approximately 50 of them are in the body of any one of your brothers or sisters.

You can do the same kind of calculation for any degree of kinship you like. An important relationship is that between parent and child. If you have one copy of gene *H*, the chance that any particular one of your children has it is 50 per cent, because half your sex cells contain *H*, and any particular child was made from one of those sex cells. If you have one copy of gene *J*, the chance that your father also had *J* is 50 per cent, because you received half your genes from him, and half from your mother. For convenience we use an index of *relatedness*, which expresses the chance of a gene being shared between two relatives. The relatedness between two brothers is ½, since half the genes possessed by one brother will be found in the other. This is an average figure: by the luck of the meiotic draw, it is possible for particular pairs of brothers to share more or fewer genes than this. The relatedness between parent and child is always exactly ½.

It is rather tedious going through the calculations from first principles every time, so here is a rough and ready rule for working out the relatedness between any two individuals *A* and *B*. You may find it useful in making your will, or in interpreting apparent resemblances in your own family. It works for all simple cases, but breaks down where incestuous mating occurs, and in certain insects, as we shall see.

First identify all the *common ancestors* of *A* and *B*. For instance, the common ancestors of a pair of first cousins are their shared grandfather and grandmother. Once you have found a common ancestor, it is of course logically true that all his ancestors are common to *A* and

B as well. However, we ignore all but the most recent common ancestors. In this sense, first cousins have only two common ancestors. If *B* is a lineal descendant of *A*, for instance his great grandson, then *A* himself is the 'common ancestor' we are looking for.

Having located the common ancestor(s) of *A* and *B*, count the *generation distance* as follows. Starting at *A*, climb up the family tree until you hit a common ancestor, and then climb down again to *B*. The total number of steps up the tree and then down again is the generation distance. For instance, if *A* is *B*'s uncle, the generation distance is 3. The common ancestor is *A*'s father (say) and *B*'s grandfather. Starting at *A* you have to climb up one generation in order to hit the common ancestor. Then to get down to *B* you have to descend two generations on the other side. Therefore the generation distance is $1 + 2 = 3$.

Having found the generation distance between *A* and *B* via a particular common ancestor, calculate that part of their relatedness for which that ancestor is responsible. To do this, multiply $\frac{1}{2}$ by itself once for each step of the generation distance. If the generation distance is 3, this means calculate $\frac{1}{2} \times \frac{1}{2} \times \frac{1}{2}$ or $(\frac{1}{2})^3$. If the generation distance via a particular ancestor is equal to *g* steps, the portion of relatedness due to that ancestor is $(\frac{1}{2})^g$.

But this is only part of the relatedness between *A* and *B*. If they have more than one common ancestor we have to add on the equivalent figure for each ancestor. It is usually the case that the generation distance is the same for all common ancestors of a pair of individuals. Therefore, having worked out the relatedness between *A* and *B* due to any one of the ancestors, all you have to do in practice is to multiply by the number of ancestors. First cousins, for instance, have two common ancestors, and the generation distance via each one is 4. Therefore their relatedness is $2 \times (\frac{1}{2})^4 = \frac{1}{8}$. If *A* is *B*'s great-grandchild, the generation distance is 3 and the number of common 'ancestors' is 1 (*B* himself), so the relatedness is $1 \times (\frac{1}{2})^3 = \frac{1}{8}$. Genetically speaking, your first cousin is equivalent to a great-grandchild. Similarly, you are just as likely to 'take after' your uncle (relatedness $= 2 \times (\frac{1}{2})^3 = \frac{1}{4}$) as after your grandfather (relatedness $= 1 \times (\frac{1}{2})^2 = \frac{1}{4}$).

For relationships as distant as third cousin ($2 \times (\frac{1}{2})^8 = \frac{1}{128}$), we are getting down near the baseline probability that a particular gene possessed by *A* will be shared by any random individual taken from the population. A third cousin is not far from being equivalent to any old Tom, Dick, or Harry as far as an altruistic gene is concerned. A second cousin (relatedness $= \frac{1}{32}$) is only a little bit special; a first cousin somewhat more so ($\frac{1}{8}$). Full brothers and sisters, and parents and children are very special ($\frac{1}{2}$), and identical twins (relatedness $= 1$) just as special as oneself. Uncles and aunts, nephews and nieces, grandparents and grandchildren, and half brothers and half sisters, are intermediate with a relatedness of $\frac{1}{4}$.

Now we are in a position to talk about genes for kin-altruism much more precisely. A gene for suicidally saving five cousins would not become more numerous in the population, but a gene for saving five brothers or ten first cousins would. The minimum requirement for a suicidal altruistic gene to be successful is that it should save more than two siblings (or children or parents), or more than four half-siblings (or uncles, aunts, nephews, nieces, grandparents, grandchildren), or more than eight first cousins, etc. Such a gene, on average, tends to live on in the bodies of enough individuals saved by the altruist to compensate for the death of the altruist itself.

If an individual could be sure that a particular person was his identical twin, he should be exactly as concerned for his twin's welfare as for his own. Any gene for twin altruism is bound to be carried by both twins, therefore if one dies heroically to save the other the gene lives on. Nine-banded armadillos are born in a litter of identical quadruplets. As far as I know, no feats of heroic self-sacrifice have been reported for young armadillos, but it has been pointed out that some strong altruism is definitely to be expected, and it would be well worth somebody's while going out to South America to have a look.*

We can now see that parental care is just a special case of kin altruism. Genetically speaking, an adult should devote just as much care and attention to its orphaned baby brother as it does to one of its own children. Its relatedness to both infants is exactly the same, $\frac{1}{2}$. In gene selection terms, a gene for big sister altruistic behaviour should have just as good a chance of spreading through the population as a gene for parental altruism. In practice, this is an over-simplification for various reasons which we shall come to later, and brotherly or sisterly care is nothing like so common in nature as parental care. But the point I am making here is that there is nothing special *genetically* speaking about the parent/child relationship as against the brother/sister relationship. The fact that parents actually hand on genes to children, but sisters do not hand on genes to each other is irrelevant, since the sisters both receive identical replicas of the same genes from the same parents.

Some people use the term *kin selection* to distinguish this kind of natural selection from group selection (the differential survival of groups) and individual selection (the differential survival of individuals). Kin selection accounts for within-family altruism; the closer the relationship, the stronger the selection. There is nothing wrong with this term, but unfortunately it may have to be abandoned because of recent gross misuses of it, which are likely to muddle and confuse biologists for years to come. E. O. Wilson, in his otherwise admirable *Sociobiology: The New Synthesis*, defines kin selection as a special case of group selection. He has a diagram which clearly shows that he thinks of it as intermediate between 'individual selection', and 'group selection' in the conventional sense—the sense that I used in Chapter 1. Now group selection—even by Wilson's own definition—means the differential survival of *groups* of individuals. There is, to be sure, a sense in which a family is a special kind of group. But the whole point of Hamilton's argument is that the distinction between family and non-family is not hard and fast, but a matter of mathematical probability. It is no part of Hamilton's theory that animals should behave altruistically towards all 'members of the family', and selfishly to everybody else. There are no definite lines to be drawn between family and non-family. We do not have to decide whether, say, second cousins should count as inside the family group or outside it: we simply expect that second cousins should be $\frac{1}{16}$ as likely to receive altruism as offspring or siblings. Kin selection is emphatically *not* a special case of group selection.* It is a special consequence of gene selection.

There is an even more serious shortcoming in Wilson's definition of kin selection. He deliberately excludes offspring: they don't count as kin!* Now of course he knows perfectly well that offspring are kin to their parents, but he prefers not to invoke the theory of kin selection in order to explain altruistic care by parents of their own offspring. He is, of course, entitled to define a word however he likes, but this is a most confusing definition, and I hope that Wilson will change it in future editions of his justly influential book. Genetically speaking, parental care and brother/sister altruism evolve for exactly the same reason: in both cases there is a good chance that the altruistic gene is present in the body of the beneficiary.

I ask the general reader's indulgence for this little diatribe, and return hastily to the main story. So far, I have over-simplified somewhat, and it is now time to introduce some qualifications. I have talked in elemental terms of suicidal genes for saving the lives of particular numbers of kin of exactly known relatedness. Obviously, in real life, animals cannot be expected to count exactly how many relatives they are saving, nor to perform Hamilton's calculations in their heads even if they had some way of knowing exactly who their brothers and cousins were. In real life, certain suicide and absolute 'saving' of life must be replaced by *statistical risks* of death, one's own and other people's. Even a third cousin may be worth saving, if the risk to yourself is very small. Then again, both you and the relative you are thinking of saving are going to die one day in any case. Every individual has an 'expectation of life' which an actuary could calculate with a certain probability of error. To save the life of a relative who is soon going to die of old age has less of an impact on the gene pool of the future than to save the life of an equally close relative who has the bulk of his life ahead of him.

Our neat symmetrical calculations of relatedness have to be modified by messy actuarial weightings. Grandparents and grandchildren have, genetically speaking, equal reason to behave altruistically to each other, since they share $\frac{1}{4}$ of each other's genes. But if the grandchildren have the greater expectation of life, genes for grandparent to grandchild altruism have a higher selective advantage than genes for grandchild to grandparent altruism. It is quite possible for the net benefit of assisting a young distant relative to exceed the net benefit of assisting an old close relative. (Incidentally, it is not, of course, necessarily the case that grandparents have a shorter expectation of life than grandchildren. In species with a high infant-mortality rate, the reverse may be true.)

To extend the actuarial analogy, individuals can be thought of as life-insurance underwriters. An individual can be expected to invest or risk a certain proportion of his own assets in the life of another individual. He takes into account his relatedness to the other individual, and also whether the individual is a 'good risk' in terms of his life expectancy compared with the insurer's own. Strictly we should say 'reproduction expectancy' rather than 'life expectancy', or to be even more strict, 'general capacity to benefit own genes in the future expectancy'. Then in order for altruistic behaviour to evolve, the net risk to the altruist must be less than the net benefit to the recipient multiplied by the relatedness. Risks and benefits have to be calculated in the complex actuarial way I have outlined.

But what a complicated calculation to expect a poor survival machine to do, especially in a hurry!* Even the great mathematical biologist J. B. S. Haldane (in a paper of 1955 in which he anticipated Hamilton by postulating the spread of a gene for saving close relatives from drowning) remarked: '... on the two occasions when I have pulled possibly drowning people out of the water (at an infinitesimal risk to myself) I had no time to make such calculations.' Fortunately, however, as Haldane well knew, it is not necessary to assume that survival machines do the sums consciously in their heads. Just as we may use a slide rule without appreciating that we are, in effect, using logarithms, so an animal may be pre-programmed in such a way that it behaves *as if* it had made a complicated calculation.

This is not so difficult to imagine as it appears. When a man throws a ball high in the air and catches it again, he behaves as if he had solved a set of differential equations in predicting the trajectory of the ball. He may neither know nor care what a differential equation is, but this does not affect his skill with the ball. At some subconscious level, something functionally equivalent to the mathematical calculations is going on. Similarly, when a man takes a difficult decision, after weighing up all the pros and cons, and all the consequences of the decision that he can imagine, he is doing the functional equivalent of a large 'weighted sum' calculation, such as a computer might perform.

If we were to program a computer to simulate a model survival machine making decisions about whether to behave altruistically, we should probably proceed roughly as follows. We should make a list of all the alternative things the animal might do. Then for each of these alternative behaviour patterns we program a weighted sum calculation. All the various benefits will have a plus sign; all the risks will have a minus sign; both benefits and risks will be *weighted* by being multiplied by the appropriate index of relatedness before being added up. For simplicity we can, to begin with, ignore other weightings, such as those for age and health. Since an individual's 'relatedness' with himself is 1 (i.e. he has 100 per cent of his own genes—obviously), risks and benefits to himself will not be devalued at all, but will be given their full weight in the calculation. The whole sum for any one of the alternative behaviour patterns will look like this: Net benefit of behaviour pattern = Benefit to self − Risk to self + $\frac{1}{2}$ Benefit to brother − $\frac{1}{2}$ Risk to brother + $\frac{1}{2}$ Benefit to other brother − $\frac{1}{2}$ Risk to other brother + $\frac{1}{8}$ Benefit to first cousin − $\frac{1}{8}$ Risk to first cousin + $\frac{1}{2}$ Benefit to child − $\frac{1}{2}$ Risk to child + etc.

The result of the sum will be a number called the net benefit score of that behaviour pattern. Next, the model animal computes the equivalent sum for each alternative behaviour pattern in his repertoire. Finally he chooses to perform the behaviour pattern which emerges with the largest net benefit. Even if all the scores come out negative, he should still choose the action with the highest one, the least of evils. Remember that any positive action involves consumption of energy and time, both of which could have been spent doing other things. If doing nothing emerges as the 'behaviour' with the highest net benefit score, the model animal will do nothing.

Here is a very over-simplified example, this time expressed in the form of a subjective soliloquy rather than a computer simulation. I am an animal who has found a clump of eight mushrooms. After taking account of their nutritional value, and subtracting something for the slight risk that they might be poisonous, I estimate that they are worth +6 units each (the units are arbitrary pay-offs as in the previous chapter). The mushrooms are so big I could eat only three of them. Should I inform anybody else about my find, by giving a 'food call'? Who is within earshot? Brother *B* (his relatedness to me is $\frac{1}{2}$), cousin *C* (relatedness to me = $\frac{1}{8}$), and *D* (no particular relation: his relatedness to me is some small number which can be treated as zero for practical purposes). The net benefit score to me if I keep quiet about my find will be +6 for each of the three mushrooms I eat, that is +18 in all. My net benefit score if I give the food call needs a bit of figuring. The eight mushrooms will be shared equally between the four of us. The pay-off to me from the two that I eat myself will be the full +6 units each, that is +12 in all. But I shall also get some pay-off when my brother and cousin eat their two mushrooms each, because of our shared genes. The actual score comes to $(1 \times 12) + (\frac{1}{2} \times 12) + (\frac{1}{8} \times 12) + (0 \times 12) = +19\frac{1}{2}$. The corresponding net benefit for the selfish behaviour was +18: it is a close-run thing, but the verdict is clear. I should give the food call; altruism on my part would in this case pay my selfish genes.

I have made the simplifying assumption that the individual animal works out what is best for his genes. What really happens is that the gene pool becomes filled with genes that influence bodies in such a way that they behave as if they had made such calculations.

In any case the calculation is only a very preliminary first approximation to what it ideally should be. It neglects many things, including the ages of the individuals concerned. Also, if I have just had a good meal, so that I can only find room for one mushroom, the net benefit of giving the food call will be greater than it would be if I was famished. There is no end to the progressive refinements of the calculation that could be achieved in the best of all possible worlds. But real life is not lived in the best of all possible worlds. We cannot expect real animals to take every last detail into account in coming to an optimum decision. We shall have to discover, by observation and experiment in the wild, how closely real animals actually come to achieving an ideal cost–benefit analysis.

Just to reassure ourselves that we have not become too carried away with subjective examples, let us briefly return to gene language. Living bodies are machines programmed by genes that have survived. The genes that have survived have done so in conditions that tended *on average* to characterize the environment of the species in the past. Therefore 'estimates' of costs and benefits are based on past 'experience', just as they are in human decision-making. However, experience in this case has the special meaning of gene experience or, more precisely, conditions of past gene survival. (Since genes also endow survival machines with the capacity to learn, some cost–benefit estimates could be said to be taken on the basis of individual experience as well.) So long as conditions do not change too drastically, the estimates will be good estimates, and survival machines will tend to make the right decisions on average. If conditions change radically, survival machines will tend to make erroneous decisions, and their genes will pay the penalty. Just so; human decisions based on outdated information tend to be wrong.

Estimates of relatedness are also subject to error and uncertainty. In our over-simplified calculations so far, we have talked as if survival machines *know* who is related to them, and how closely. In real life such certain knowledge is occasionally possible, but more usually the relatedness can only be estimated as an average number. For example, suppose that *A* and *B* could equally well be either half brothers or full brothers. Their relatedness is either $\frac{1}{4}$ or $\frac{1}{2}$, but since we do not know whether they are half or full brothers, the effectively usable figure is the average, $\frac{3}{8}$. If it is certain that they have the same mother, but the odds that they have the same father are only 1 in 10, then it is 90 per cent certain that they are half brothers, and 10 per cent certain that they are full brothers, and the effective relatedness is $\frac{1}{10} \times \frac{1}{2} + \frac{9}{10} \times \frac{1}{4} = 0{\cdot}275$.

But when we say something like 'it' is 90 per cent certain, what 'it' are we referring to? Do we mean a human naturalist after a long field study is 90 per cent certain, or do we mean the animals are 90 per cent certain? With a bit of luck these two may amount to nearly the same thing. To see this, 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, because we give them names, because we have formal marriages, and because we have written records and good memories. Many social anthropologists are preoccupied with 'kinship' in the societies which they study. They do not mean real genetic kinship, but subjective and cultural ideas of kinship. Human customs and tribal rituals commonly give great emphasis to kinship; ancestor worship is widespread, family obligations and loyalties dominate much of life. Blood-feuds and inter-clan warfare are easily interpretable in terms of Hamilton's genetic theory. Incest taboos testify to the great kinship-consciousness of man, although the genetical advantage of an incest taboo is nothing to do with altruism; it is presumably concerned with the injurious effects of recessive genes which appear with inbreeding. (For some reason many anthropologists do not like this explanation.)*

How could wild animals 'know' who their kin are, or in other words, what behavioural rules could they follow which would have the indirect effect of making them seem to know about kinship? The rule 'be nice to your relations' begs the question of how relations are to be recognized in practice. Animals have to be given by their genes a simple rule for action, a rule that does not involve all-wise cognition of the ultimate purpose of the action, but a rule that works nevertheless, at least in average conditions. We humans are familiar with rules, and so powerful are they that if we are small minded we obey a rule itself, even when we can see perfectly well that it is not doing us, or anybody else, any good. For instance, some orthodox Jews and Muslims would starve rather than break their rule against eating pork. What simple practical rules could animals obey which, under normal conditions, would have the indirect effect of benefiting their close relations?

If animals had a tendency to behave altruistically towards individuals who physically resembled them, they might indirectly be doing their kin a bit of good. Much would depend on details of the species concerned. Such a rule would, in any case, only lead to 'right' decisions in a statistical sense. 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.

In a species whose members do not move around much, or whose members move around in small groups, the chances may be good that any random individual you come across is fairly close kin to you. In this case the rule 'Be nice to any member of the species whom you meet' could have positive survival value, in the sense that a gene predisposing its possessors to obey the rule might become more numerous in the gene pool. This may be why altruistic behaviour is so frequently reported in troops of monkeys and schools of whales. Whales and dolphins drown if they are not allowed to breathe air. Baby whales, and injured individuals who cannot swim to the surface have been seen to be rescued and held up by companions in the school. It is not known whether whales have ways of knowing who their close relatives are, but it is possible that it does not matter. It may be that the overall probability that a random member of the school is a relation is so high that the altruism is worth the cost. Incidentally, there is at least one well-authenticated story of a drowning human swimmer being rescued by a wild dolphin. This could be regarded as a misfiring of the rule for saving drowning members of the school. The rule's 'definition' of a member of the school who is drowning might be something like: 'A long thing thrashing about and choking near the surface.'

Adult male baboons have been reported to risk their lives defending the rest of the troop against predators such as leopards. It is quite probable that any adult male has, on average, a fairly large number of genes tied up in other members of the troop. A gene that 'says', in effect: 'Body, if you happen to be an adult male, defend the troop against leopards', could become more numerous in the gene pool. Before leaving this often-quoted example, it is only fair to add that at least one respected authority has reported very different facts. According to her, adult males are the first over the horizon when a leopard appears.

Baby chicks feed in family clutches, all following their mother.

They have two main calls. In addition to the loud piercing cheep which I have already mentioned, they give short melodious twitters when feeding. The cheeps, which have the effect of summoning the mother's aid, are ignored by the other chicks. The twitters, however, are attractive to chicks. This means that when one chick finds food, its twitters attract other chicks to the food as well: in the terms of the earlier hypothetical example, the twitters are 'food calls'. As in that case, the apparent altruism of the chicks can easily be explained by kin selection. Since, in nature, the chicks would be all full brothers and sisters, a gene for giving the food twitter would spread, provided the cost to the twitterer is less than half the net benefit to the other chicks. As the benefit is shared out between the whole clutch, which normally numbers more than two, it is not difficult to imagine this condition being realized. Of course the rule misfires in domestic or farm situations when a hen is made to sit on eggs not her own, even turkey or duck eggs. But neither the hen nor her chicks can be expected to realize this. Their behaviour has been shaped under the conditions that normally prevail in nature, and in nature strangers are not normally found in your nest.

Mistakes of this sort may, however, occasionally happen in nature. In species that live in herds or troops, an orphaned youngster may be adopted by a strange female, most probably one who has lost her own child. Monkey-watchers sometimes use the word 'aunt' for an adopting female. In most cases there is no evidence that she really is an aunt, or indeed any kind of relative: if monkey-watchers were as gene-conscious as they might be, they would not use an important word like 'aunt' so uncritically. In most cases we should probably regard adoption, however touching it may seem, as a misfiring of a built-in rule. This is because the generous female is doing her own genes no good by caring for the orphan. She is wasting time and energy which she could be investing in the lives of her own kin, particularly future children of her own. It is presumably a mistake that happens too seldom for natural selection to have 'bothered' to change the rule by making the maternal instinct more selective. In many cases, by the way, such adoptions do not occur, and an orphan is left to die.

There is one example of a mistake which is so extreme that you may prefer to regard it not as a mistake at all, but as evidence against the selfish gene theory. This is the case of bereaved monkey mothers who have been seen to steal a baby from another female, and look after it. I see this as a double mistake, since the adopter not only wastes her own time; she also releases a rival female from the burden of child-rearing, and frees her to have another child more quickly. It seems to me a critical example which deserves some thorough research. We need to know how often it happens; what the average relatedness between adopter and child is likely to be; and what the attitude of the real mother of the child is—it is, after all, to her advantage that her child *should* be adopted; do mothers deliberately try to deceive naïve young females into adopting their children? (It has also been suggested that adopters and baby-snatchers might benefit by gaining valuable practice in the art of child-rearing.)

An example of a deliberately engineered misfiring of the maternal instinct is provided by cuckoos, and other 'brood-parasites'—birds that lay their eggs in somebody else's nest. Cuckoos exploit the rule built into bird parents: 'Be nice to any small bird sitting in the nest that you built.' Cuckoos apart, this rule will normally have the desired effect of restricting altruism to immediate kin, because it happens to be a fact that nests are so isolated from each other that the contents of your own nest are almost bound to be your own chicks. Adult herring gulls do not recognize their own eggs, and will happily sit on other gull eggs, and even crude wooden dummies if these are substituted by a human experimenter. In nature, egg recognition is not important for gulls, because eggs do not roll far enough to reach the vicinity of a neighbour's nest, some yards away. Gulls do, however, recognize their own chicks: chicks, unlike eggs, wander, and can easily end up near the nest of a neighbouring adult, often with fatal results, as we saw in Chapter 1.

Guillemots, on the other hand, do recognize their own eggs by means of the speckling pattern, and actively discriminate in favour of them when incubating. This is presumably because they nest on flat rocks, where there is a danger of eggs rolling around and getting muddled up. Now, it might be said, why do they bother to discriminate and sit only on their own eggs? Surely if everybody saw to it that she sat on somebody's egg, it would not matter whether each particular mother was sitting on her own or somebody else's. This is the argument of a group selectionist. Just consider what would happen if such a group baby-sitting circle did develop. The average clutch size of the guillemot is one. This means that if the mutual baby-sitting circle is to work successfully, every adult would have to sit on an average of one egg. Now suppose somebody cheated, and refused to sit on an egg. Instead of wasting time sitting, she could spend her time laying more eggs. And the beauty of the scheme is that the other, more altruistic, adults would look after them for her. They would go on faithfully obeying the rule 'If you see a stray egg near your nest, haul it in and sit on it.' So the gene for cheating the system would spread through the population, and the nice friendly baby-sitting circle would break down.

'Well', it might be said, 'what if the honest birds retaliated by refusing to be blackmailed, and resolutely decided to sit on one egg and only one egg? That should foil the cheaters, because they would see their own eggs lying out on the rocks with nobody incubating them. That should soon bring them into line.' Alas, it would not. Since we are postulating that the sitters are not discriminating one egg from another, if the honest birds put into practice this scheme for resisting cheating, the eggs that ended up being neglected would be just as likely to be their own eggs as those of the cheaters. The cheaters would still have the advantage, because they would lay more eggs and have more surviving children. The only way an honest guillemot could beat the cheaters would be to discriminate actively in favour of her own eggs. That is, to cease being altruistic and look after her own interests.

To use the language of Maynard Smith, the altruistic adoption 'strategy' is not an evolutionarily stable strategy. It is unstable in the sense that it can be bettered by a rival selfish strategy of laying more than one's fair share of eggs, and then refusing to sit on them. This latter selfish strategy is in its turn unstable, because the altruistic strategy which it exploits is unstable, and will disappear. The only evolutionarily stable strategy for a guillemot is to recognize its own egg, and sit exclusively on its own egg, and this is exactly what happens.

The song-bird species that are parasitized by cuckoos have fought back, not in this case by learning the appearance of their own eggs, but by discriminating instinctively in favour of eggs with the species-typical markings. Since they are not in danger of being parasitized by members of their own species, this is effective.* But the cuckoos have retaliated in their turn by making their eggs more and more like those of the host species in colour, size, and markings. This is an example of a lie, and it often works. The result of this evolutionary arms race has been a remarkable perfection of mimicry on the part of the cuckoo eggs. We may suppose that a proportion of cuckoo eggs and chicks are 'found out', and those that are not found out are the ones who live to lay the next generation of cuckoo eggs. So genes for more effective deception spread through the cuckoo gene pool. Similarly, those host birds with eyes sharp enough to detect any slight imperfection in the cuckoo eggs' mimicry are the ones that contribute most to their own gene pool. Thus sharp and sceptical eyes are passed on to their next generation. This is a good example of how natural selection can sharpen up active discrimination, in this case discrimination against another species whose members are doing their best to foil the discriminators.

Now let us return to the comparison between an animal's 'estimate' of its kinship with other members of its group, and the corresponding estimate of an expert field naturalist. Brian Bertram has spent many years studying the biology of lions in the Serengeti National Park. On the basis of his knowledge of their reproductive habits, he has estimated the average relatedness between individuals in a typical lion pride. The facts that he uses to make his estimates are things like this. A typical pride consists of seven adult females who are its more permanent members, and two adult males who are itinerant. About half the adult females give birth as a batch at the same time, and rear their cubs together so that it is difficult to tell which cub belongs to whom. The typical litter size is three cubs. The fathering of litters is shared equally between the adult males in the pride. Young females remain in the pride and replace old females who die or leave. Young males are driven out when adolescent. When they grow up, they wander around from pride to pride in small related gangs or pairs, and are unlikely to return to their original family.

Using these and other assumptions, you can see that it would be possible to compute an average figure for the relatedness of two individuals from a typical lion pride. Bertram arrives at a figure of 0·22 for a pair of randomly chosen males, and 0·15 for a pair of females. That is to say, males within a pride are on average slightly less close than half brothers, and females slightly closer than first cousins.

Now, of course, any particular pair of individuals might be full brothers, but Bertram had no way of knowing this, and it is a fair bet that the lions did not know it either. On the other hand, the average figures that Bertram estimated are available to the lions themselves in a certain sense. If these figures really are typical for an average lion pride, then any gene that predisposed males to behave towards other males as if they were nearly half brothers would have positive survival value. Any gene that went too far and made males behave in a friendly way more appropriate to full brothers would on average be penalized, as would a gene for not being friendly enough, say treating other males like second cousins. If the facts of lion life are as Bertram says, and, just as important, if they have been like that for a large number of generations, then we may expect that natural selection will have favoured a degree of altruism appropriate to the average degree of relatedness in a typical pride. This is what I meant when I said that the kinship estimates of animal and of good naturalist might end up rather the same.*

So we conclude that the 'true' relatedness may be less important in the evolution of altruism than the best *estimate* of relatedness that animals can get. This fact is probably a key to understanding why parental care is so much more common and more devoted than brother/sister altruism in nature, and also why animals may value themselves more highly even than several brothers. Briefly, what I am saying is that, in addition to the index of relatedness, we should consider something like an index of 'certainty'. Although the parent/child relationship is no closer genetically than the brother/sister relationship, its certainty is greater. It is normally possible to be much more certain who your children are than who your brothers are. And you can be more certain still who you yourself are!

We considered cheaters among guillemots, and we shall have more to say about liars and cheaters and exploiters in following chapters. In a world where other individuals are constantly on the alert for opportunities to exploit kin-selected altruism, and use it for their own ends, a survival machine has to consider who it can trust, who it can be really sure of. *If B* is really my baby brother, then I should care for him up to half as much as I care for myself, and fully as much as I care for my own child. But can I be as sure of him as I can of my own child? How do I know he is my baby brother?

If C is my identical twin, then I should care for him twice as much as I care for any of my children, indeed I should value his life no less than my own.* But can I be sure of him? He looks like me to be sure, but it could be that we just happen to share the genes for facial features. No, I will not give up my life for him, because although it is *possible* that he bears 100 per cent of my genes, I absolutely *know* that

I contain 100 per cent of my genes, so I am worth more to me than he is. I am the only individual that any one of my selfish genes can be sure of. And although ideally a gene for individual selfishness could be displaced by a rival gene for altruistically saving at least one identical twin, two children or brothers, or at least four grandchildren etc., the gene for individual selfishness has the enormous advantage of *certainty* of individual identity. The rival kin-altruistic gene runs the risk of making mistakes of identity, either genuinely accidental, or deliberately engineered by cheats and parasites. We therefore must expect individual selfishness in nature, to an extent greater than would be predicted by considerations of genetic relatedness alone.

In many species a mother can be more sure of her young than a father can. The mother lays the visible, tangible egg, or bears the child. She has a good chance of knowing for certain the bearers of her own genes. The poor father is much more vulnerable to deception. It is therefore to be expected that fathers will put less effort than mothers into caring for young. We shall see that there are other reasons to expect the same thing, in the chapter on the Battle of the Sexes (Chapter 9). Similarly, maternal grandmothers can be more sure of their grandchildren than paternal grandmothers can, and might be expected to show more altruism than paternal grandmothers. This is because they can be sure of their daughter's children, but their son may have been cuckolded. Maternal grandfathers are just as sure of their grandchildren as paternal grandmothers are, since both can reckon on one generation of certainty and one generation of uncertainty. Similarly, uncles on the mother's side should be more interested in the welfare of nephews and nieces than uncles on the father's side, and in general should be just as altruistic as aunts are. Indeed 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. They know that the child's mother is at least their half-sister. The 'legal' father knows nothing. I do not know of any evidence bearing on these predictions, but I offer them in the hope that others may, or may start looking for evidence. In particular, perhaps social anthropologists might have interesting things to say.*

Returning to the fact that parental altruism is more common than fraternal altruism, it does seem reasonable to explain this in terms of the 'identification problem'. But this does not explain the fundamental asymmetry in the parent/child relationship itself. Parents care more for their children than children do for their parents, although the genetic relationship is symmetrical, and certainty of relatedness is just as great both ways. One reason is that parents are in a better practical position to help their young, being older and more competent at the business of living. Even if a baby wanted to feed its parents, it is not well equipped to do so in practice.

There is another asymmetry in the parent/child relationship which does not apply to the brother/sister one. Children are always younger than their parents. This often, though not always means they have a longer expectation of life. As I emphasized above, expectation of life is an important variable which, in the best of all possible worlds, should enter into an animal's 'calculation' when it is 'deciding' whether to behave altruistically or not. In a species in which children have a longer average life expectancy than parents, any gene for child altruism would be labouring under a disadvantage. It would be engineering altruistic self-sacrifice for the benefit of individuals who are nearer to dying of old age than the altruist itself. A gene for parent altruism, on the other hand, would have a corresponding advantage as far as the life-expectancy terms in the equation were concerned.

One sometimes hears it said that kin selection is all very well as a theory, but there are few examples of its working in practice. This criticism can only be made by someone who does not understand what kin selection means. The truth is that all examples of child-protection and parental care, and all associated bodily organs, milk-secreting glands, kangaroo pouches, and so on, are examples of the working in nature of the kin-selection principle. The critics are of course familiar with the widespread existence of parental care, but they fail to understand that parental care is no less an example of kin selection than brother/sister altruism. When they say they want examples, they mean that they want examples other than parental care, and it is true that such examples are less common. I have suggested reasons why this might be so. I could have gone out of my way to quote examples of brother/sister altruism—there are in fact quite a few. But I don't want to do this, because it would reinforce the erroneous idea (favoured, as we have seen, by Wilson) that kin selection is specifically about relationships *other than* the parent/child relationship.

The reason this error has grown up is largely historical. The evolutionary advantage of parental care is so obvious that we did not have to wait for Hamilton to point it out. It has been understood ever since Darwin. When Hamilton demonstrated the genetic equivalence of other relationships, and their evolutionary significance, he naturally had to lay stress on these other relationships. In particular, he drew examples from the social insects such as ants and bees, in which the sister/sister relationship is particularly important, as we shall see in a later chapter. I have even heard people say that they thought Hamilton's theory applied *only* to the social insects!

If anybody does not want to admit that parental care is an example of kin selection in action, then the onus is on him to formulate a general theory of natural selection that predicts parental altruism, but that does *not* predict altruism between collateral kin. I think he will fail.

7

Family planning

It is easy to see why some people have wanted to separate parental care from the other kinds of kin-selected altruism. Parental care looks like an integral part of reproduction whereas, for example, altruism toward a nephew is not. I think there really is an important distinction hidden here, but that people have mistaken what the distinction is. They have put reproduction and parental care on one side, and other sorts of altruism on the other. But I wish to make a distinction between *bringing new individuals into the world*, on the one hand, and *caring for existing individuals* on the other. I shall call these two activities respectively child-bearing and child-caring. An individual survival machine has to make two quite different sorts of decisions, caring decisions and bearing decisions. I use the word decision to mean unconscious strategic move. The caring decisions are of this form: 'There is a child; its degree of relatedness to me is so and so; its chances of dying if I do not feed it are such and such; shall I feed it?' Bearing decisions, on the other hand, are like this: 'Shall I take whatever steps are necessary in order to bring a new individual into the world; shall I reproduce?' To some extent, caring and bearing are bound to compete with each other for an individual's time and other resources: the individual may have to make a choice: 'Shall I care for this child or shall I bear a new one?'

Depending on the ecological details of the species, various mixes of caring and bearing strategies can be evolutionarily stable. The one thing that cannot be evolutionarily stable is a *pure* caring strategy. If all individuals devoted themselves to caring for existing children to such an extent that they never brought any new ones into the world, the population would quickly become invaded by mutant individuals who specialized in bearing. Caring can only be evolutionarily stable as part of a mixed strategy—at least some bearing has to go on.

The species with which we are most familiar—mammals and birds—tend to be great carers. A decision to bear a new child is