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The Paradox of Altruism

Darwin's Insuperable Difficulty

As we have already seen, the sterile worker bee strives to rear the queen's brood and usually dies without herself reproducing. And the worker bee is exquisitely adapted to perform her tasks. She has wax glands in her abdomen, pollen baskets on her hind legs, and the ability to perform an elaborate dance language to recruit nestmate workers to new sources of food. The queen bee has none of these abilities. How can natural selection favor the sterile honey bee worker that leaves behind no offspring or even the squirrel that reduces its chances of survival by giving an alarm call upon seeing a predator? More paradoxical, perhaps, how can the process of natural selection help perfect the adaptations of the sterile worker bee? We couldn't say, for example, that workers who had better pollen baskets left behind more offspring and gradually replaced those workers who had inferior pollen baskets. Only the queen reproduces and natural selection can only act on her.

It is a tribute to the genius of Charles Darwin that these questions bothered him, but I do not believe that he had a satisfactory answer. In *On the Origin of Species* Darwin referred to the worker honey bee as a

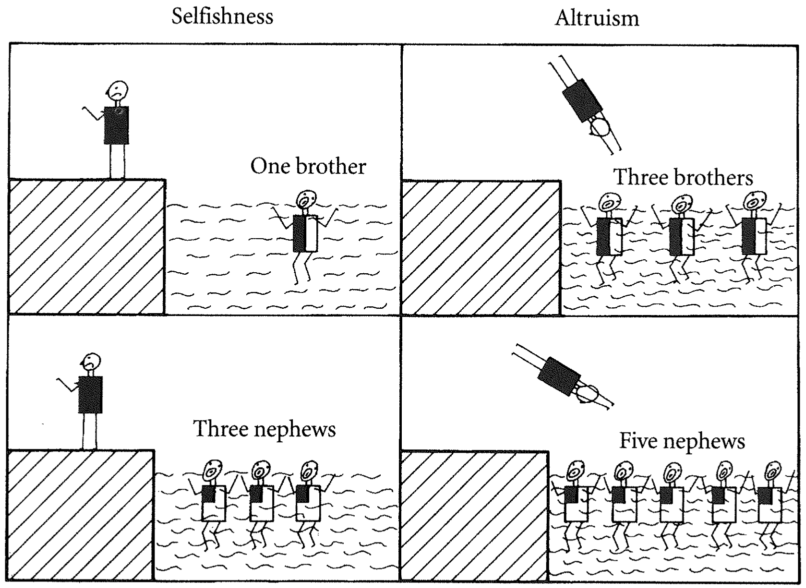
"special difficulty, which first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters or sterile females in insect communities: for these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind." Two paragraphs later Darwin summarizes his solution to the problem: "This difficulty though appearing insuperable, is lessened, or, as I believe disappears, when it is remembered that selection may be applied to the family, as well as to the individual and may thus gain the desired end. Thus a well-flavored vegetable is cooked, and the individual is destroyed; but the horticulturist sows seed of the same stock, and confidently expects to get nearly the same variety; breeders of cattle wish the flesh and fat to be well marbled together; the animal has been slaughtered, but the breeder goes with confidence to the same family."

Historians have now suggested that Darwin's analogy with artificial selection of cattle does not ring true; perhaps it didn't quite satisfy Darwin himself. Darwin delayed the publication of his theory of natural selection for years and might have delayed it even further if Alfred Russel Wallace had not independently hit upon the idea and thereby spurred Darwin to publish. Writing in the *Journal of the History of Biology*, F. R. Prete has described "the conundrum of the honey bees" as "one impediment to the publication of Darwin's theory." Prete's point is that unlike the queen and worker bees, the slaughtered cow and the cattle used for breeding are both almost identical and that is why the breeder goes with confidence to the same family. The worker bee is quite different from both the queen and the drone, and yet nature appears to go with confidence to the queens and drones of hives containing workers with superior pollen baskets to get more workers with superior pollen baskets. To make Darwin's analogy with cattle apply to the bees, we have to imagine, in Prete's words, that "a cattle breeder has a skinny pure white cow and an ugly pure black bull. When bred, these animals invariably give rise to large herds of beautiful, brown, quality beef cattle, all of one sex, and an occasional pair of breeders (one skinny white and the other ugly black) who could repeat the process." Not surprisingly, Prete concludes that "it is highly improbable that Darwin, as insightful and meticulous as he was, did not also consider this difficulty."

When Would You Risk Your Life to Save a Child?

John Burdon Sanderson Haldane was a truly remarkable man. John Maynard Smith, his student and colleague, writes of him: although "Haldane will be remembered for his contribution to the theory of evolution . . . he is in other respects somewhat difficult to classify. A liberal individualist, he was best known as a leading communist and contributor of a weekly article to the *Daily Worker*. A double first class in classics and mathematics at Oxford, he made his name in biochemistry and genetics. A captain in the Black Watch who admitted to rather enjoying the First World War, he spent the end part of his life in India writing in defense of non-violence."

In an obscure little article that appeared in 1953 in a now defunct magazine called *Penguin New Biology*, Haldane sowed the seeds of an idea that provides a satisfactory solution to Darwin's insuperable difficulty. Before I read Haldane's article in the original, I had heard of it in the form of a story which goes something like this: Haldane was once walking on the bank of a river with a friend. As was typical of him, Haldane paused for a moment, made a quick calculation on the palm of his hand, and declared: "If one or two of my brothers were drowning in this river, I might perhaps not risk my life to save them but if more than two of my brothers were drowning, I might attempt to save them at a risk to my life." The story may be pure fiction, but I find it very useful in teaching students the modern solution to Darwin's paradox. And it no doubt faithfully reflects Haldane's written version, at least as far as the scientific idea is concerned. Haldane wrote, "Let us suppose that you carry a rare gene which affects your behavior so that you jump into a flooded river and save a child, but you have one chance in ten of being drowned . . . If the child is your own child, or your brother or sister, there is an even chance that the child will also have this gene, so five such genes will be saved in children for one lost in the adult. If you save a



Cartoon illustrating the theme of J. B. S. Haldane's story. The shaded portions of the drowning individuals indicate the proportion of their genes which are also present in the altruist standing on the bank. Notice that the altruist is willing to risk his life when the numbers of his genes expected to be rescued is greater than the number in his body likely to be lost. *(Drawing: Sudha Premnath.)*

grandchild or nephew the advantage is only two and a half to one. If you only save a first cousin, the effect is very slight. If you try to save your first cousin once removed the population is more likely to lose this valuable gene than to gain it."

The Concept of Inclusive Fitness

W. D. Hamilton has given us the required modification of Darwin's theory that can accommodate altruism. Hamilton argued that altruism is no paradox at all if we realize that natural selection is dependent on changes in the relative frequencies of genes (alleles) regardless of the pathway by which the change is brought about. What this means of course is that producing offspring is only one way to increase the representation of one's genes in the population. Aiding genetic relatives who carry copies of one's genes is another, equally legitimate, way of doing so. To put it more starkly, you can be sterile and still have fitness. But how do we decide whether a sterile individual is just as fit as or fitter than a fertile one? We have no difficulty in deciding that an individual producing two offspring is fitter than another producing only one offspring. But how do we compare the fitnesses of individuals producing one offspring and those devoting their lives to taking care of, say, one brother or three cousins or five nephews.

This is where we can go back to Haldane's logic. On the average, we share one half of our genes with our offspring and siblings, one fourth with our grandchildren and nieces and nephews, one eighth with our cousins, and so on. As far as evolution is concerned, caring for one child is equivalent to caring for one sibling, or two grandchildren, or two nephews, or four cousins, and so on. Genetically speaking, we can express any class of relatives as offspring equivalents and then compare the fitnesses of individuals with different propensities for rearing offspring or aiding relatives. Hamilton went a step further and converted everything into genome equivalents (a genome being the entire genetic material of one individual). This is easily done by multiplying the number of offspring and siblings by 0.5, the number of grandchildren and nieces and nephews by 0.25, the number of cousins by 0.125, and so on. The contribution of different classes of relatives to fitness can then be added up to yield the *inclusive fitness*. Now we can appreciate Haldane's reluctance to risk his life to save only one or two brothers and his readiness to risk his life to save three or more brothers. Being related to himself by 1.0, he would need to save three or more brothers (0.5 × 3 or more) to make up for the loss of his entire genome.

Consider another example. Praveen Karanth and S. Sridhar studied the breeding behavior of the small green bee-eater in and around Bangalore, India. They found that in about 40 percent of the birds' nests there was a helper in addition to the breeding pair. The helpers must truly help because nests with helpers produced more fledglings per nest than nests without helpers, and these fledglings grew more rapidly and had fewer problems with predation than fledglings without helpers. Karanth and Sridhar did not know the genetic relationships between the helpers and the breeding pairs. But we know from other species of birds with the helping habit that older offspring often help their parents rear a second brood. Suppose a young bee-eater that goes off to breed can produce two chicks while one that stays to help its parents contributes to the survival of three more chicks than the parents can raise without help. The inclusive fitness of the helper will be greater than that of the one that goes off to breed on its own. Notice, however, that we should credit helpers only with the additional chicks reared because of their help, and not assign fitness to them for the chicks that might have survived anyway. When we were only counting offspring it was easy to assign credit. When we also count relatives in assigning fitness, there is a danger of double counting and we must guard against it.

The Two Components of Inclusive Fitness

I study a socially primitive wasp called *Ropalidia marginata.* These wasps form social colonies with nonreproducing workers and reproductive queens. Queens and workers are not morphologically different and hence individual wasps can act as queens or workers in response to the opportunities available. I have come across some individuals who work for a time, helping their mothers to produce more offspring, and later drive out their own mothers and become queens in the same colony. How do we compute the inclusive fitness of such individuals pursuing multiple strategies? That's simple enough. We can just convert everything into genome equivalents and then add up the fitness gained through offspring and that gained through relatives. Inclusive fitness, then, has two components, a direct, individual component, gained through selfish, offspring production, and an indirect, social component, gained through altruistic caring for genetic relatives. The sum of these two components is what matters, and therefore even if one component is zero the sum may still be very large. That then is the secret of the evolutionary success of sterile honey bee workers.

It is worth emphasizing that natural selection does not, in any way, break up inclusive fitness into direct and social fitness components. Indeed, natural selection cannot distinguish between fitness gained through the direct component and fitness gained through the social component, and that is why two individuals with the same level of inclusive fitness are identical in the eyes of natural selection even though one may have gained all of its inclusive fitness through the direct component while the other may have gained it all through the social component. Then why should we break inclusive fitness up into direct and social components? Because if we want to measure the inclusive fitness of animals in real life, it is convenient and even necessary to do so. The circumstances and the strategies associated with accumulating direct fitness are often different from those associated with the acquisition of social fitness. Also, in the case of the social component, one has to worry much more about the level of genetic relatedness between the actor and the recipient, while in the case of the direct component, the relationship between parent and offspring is almost always 0.5. When a behavior is favored by natural selection exclusively or primarily because of its contribution to the social component of inclusive fitness, the behavior is said to have evolved by *kin selection.*

Hamilton's Rule

We have just derived a fundamental rule in evolutionary biology that is known as Hamilton's Rule. Stated in more technical terms, Hamilton's rule is that an altruistic trait can evolve if the number of individuals gained, multiplied by the altruist's genetic relatedness to those individuals, is greater than the number of individuals lost, multiplied by the altruist's relatedness to them. If Haldane had rescued three brothers and lost his life in the process, the number of individuals gained multiplied by his relatedness to them ($3 \times 0.5 = 1.5$) would have been greater than the number of individuals lost, namely Haldane himself, multiplied by Haldane's relatedness to himself, 1.0 ($1 \times 1.0 = 1.0$). Thus the altruistic trait of risking one's life to save some one in danger *can evolve by* natural selection, provided of course that other conditions such as a genetic basis for the behavior are met. If an altruistic bee-eater helps its parents produce an additional three sibling chicks, its inclusive fitness as a helper is the number of individuals gained times its relatedness to

Hamilton's Rule

$$b/c > 1/r$$

b = benefit to recipient
c = cost to donor
r = genetic relatedness between donor and recipient

or

$$n_i r_i > n_o r_o$$

n_i = no. of relatives reared
r_i = relatedness to relatives
n_o = no. of offspring reared
r_o = relatedness to offspring

Hamilton's rule defines the condition for the evolution of altruism. The upper form is useful to predict when an individual will be selected to sacrifice its life to help others. The lower form is useful to predict when a sterile individual who rears relatives will be selected over a fertile individual who rears offspring.

them: $3 \times 0.5 = 1.5$. If the helper had produced two offspring instead, its inclusive fitness would be the number of individuals gained multiplied by its relatedness: $2 \times 0.5 = 1.0$. Its inclusive fitness as a helper would be greater than its inclusive fitness as a breeder and hence Hamilton's rule is satisfied and the altruistic trait can evolve. Notice that we can only say that it *can* evolve; we cannot assert that it *will* evolve. The trait can only evolve if other conditions such as its having a genetic basis

are met. Our strategy will thus be to see what types of behaviors *can* evolve and what types *have* actually evolved. If what can evolve has evolved, that will be satisfying because it will suggest that we are on the right track in our theorizing. If we find that what can evolve has not evolved, and especially if what cannot evolve according to theory has evolved, we will be challenged to refine our theory.

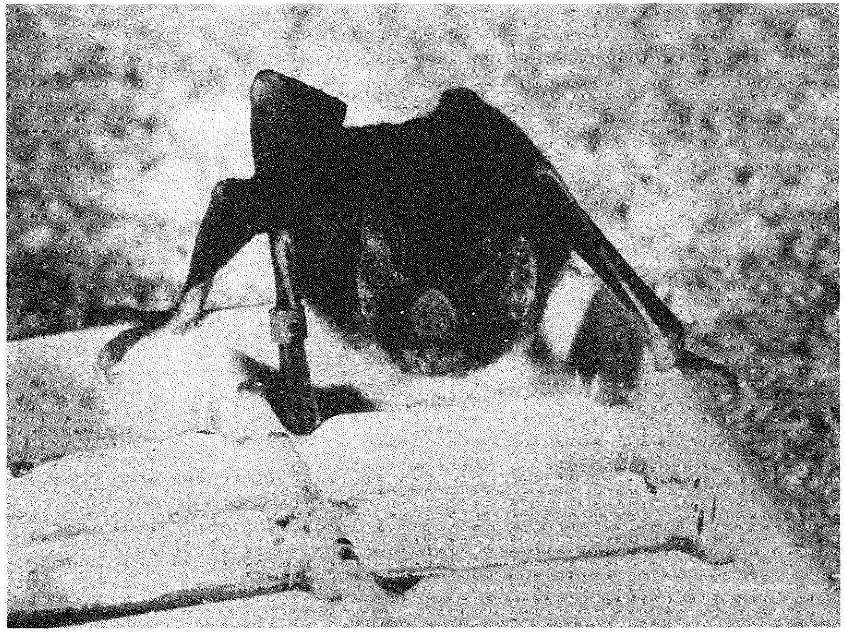
At the risk of stating the obvious, let me stress that Hamilton's rule does not just provide a theory for the evolution of altruism. It simultaneously and automatically provides a theory for the evolution of selfishness. If Haldane had risked his life to save just one brother, his inclusive fitness ($1 \times 0.5 = 0.5$) would have been less than it might have been if he had looked the other way ($1 \times 1.0 = 1.0$). If a bee-eater foregoes an opportunity to breed and becomes a helper but can only increase the number of fledged chicks in its parents' nest by one, it will similarly suffer a net loss in inclusive fitness. Under these conditions, selfishness is expected to evolve rather than altruism. Cooperation, of course, is easily explained by Hamilton's rule because it will increase the inclusive fitness of the actor without any associated cost (both actor and recipient benefit).

There is, however, a problem that at first sight appears incapable of explanation by Hamilton's rule. If we are equally related to our offspring and our siblings, why is care and attention showered so much more generously on offspring than on siblings throughout the animal kingdom? Hamilton's rule by itself appears to predict no particular preference for one over the other. But that is not true, because here we are only looking at the identical relatedness to offspring and siblings. We must also focus on the benefit and cost, and here there may be quite a difference between offspring and siblings. Animals routinely have access to young and helpless offspring at a time when they themselves are adults. The cost of helping offspring in this situation will be relatively small but the benefit to the offspring will be great. The situation is different with siblings: they are often roughly the same age and at the same level of helplessness and therefore the cost of their helping each other will be high and the benefit not so great. Thus Hamilton's rule does predict that help will be given more often to offspring than to siblings.

Reciprocal Altruism

There is yet another way altruism can evolve. Imagine you are hungry today but have no money to buy food. And if you don't eat you might actually die. I have a little more money than I need for today, but I better not give it to you because I may end up like you tomorrow, and you are not even related to me. But of course I might go hungry and be broke tomorrow even if I don't give you the extra money I have today. On second thought, I will give you the extra money I have today. Perhaps some day I will be hungry and broke and you will remember my good deed and help me out. On that day you will probably not suffer greatly by giving me your extra money, but it will make all the difference between life and death for me just as it will for you today. We will both benefit from such *reciprocal altruism*. We might both have died if we had not helped each other. Reciprocal altruism has made it possible for both of us to survive. You will see no doubt that my helping you would not have been a good idea if there was not a high probability that you would return the favor when I needed it. Thus reciprocal altruism can evolve if (1) there is a good chance that the same actors will meet repeatedly; (2) they can recognize each other; and (3) they can remember who helped them in the past and who did not. The last-mentioned condition is of utmost importance because reciprocal altruists need to guard against cheaters. Of course it is best for me to take your help when I am in trouble and avoid helping you when you are in need. Cheaters can go scot free if the conditions of repeated encounters, recognition, and memory are not met. But then the trait of helping will not pay dividends and hence will not be favored by natural selection.

The idea of the evolution of altruism by reciprocity was proposed by Robert Trivers. But do animals practice reciprocal altruism? There is at least one good example, and strangely enough it also has to do with donating extra food in times of excess to those in need. The only difference is that it concerns the sharing of extra blood by vampire bats,



The common vampire bat *Desmodus rotundus* feeding on blood provided in plastic trays in the laboratory. *(Photo: Merlin D. Tuttle, Bat Conservation International.)*

not quite what I might have given you when you were hungry. Gerald Wilkinson studied vampire bats in Costa Rica. These bats live in groups of 8 to 10 females, some of whom are sisters but some of whom are unrelated to each other. These groups of females associate with each other for 2 to 11 years and thus they have ample opportunities to indulge in reciprocal altruism. Vampire bats fly out at night to feed on the blood of cattle and horses and then return to their roosting sites to spend the day. Not all bats succeed in feeding on all nights but who succeeds and who fails appears to be a matter of chance. Bats that fail to feed on three consecutive nights will almost certainly die of starvation. Wilkinson found that hungry bats will beg food from well-fed ones and will usually be offered some blood. Bats receiving blood are more likely to donate blood when they themselves are well fed and are importuned by hungry bats. The bats groom each other on their stomachs and this appears to be their way of telling who is well fed and who is hungry. There is evidence from laboratory studies that they can remember the individuals to whom they have donated blood in the past. These bats can ingest an amount of blood equal to their body weight and hold most of it in highly distensible stomachs; this must make it very difficult for a well-fed bat to pretend, especially while being groomed on its stomach, that it has nothing to regurgitate. Thus there appears to be a reasonable mechanism to detect and punish cheaters—an essential condition for the evolution of reciprocal altruism.

Is It All Just Selfishness?

One solution I offered for the paradox of altruism is that it is no paradox at all if altruism is directed toward genetic relatives and the net gain due to the increased survival of copies of the altruist's genes through the helped relatives is greater than the loss of copies of the altruist's genes

due to its own death or a reduction in the number of its offspring. In short, apparent altruism at the level of the individual animal is no altruism at all at the level of the genes; it's really selfishness from the point of view of the genes. The second solution I offered for the apparent paradox of altruism is that altruism may be practiced because of the high probability of its being reciprocated when the giver may be in more need of help than it is now. You might argue that this is no altruism either but is instead a very clever kind of selfishness. So is all altruism really selfishness? Perhaps it is.

Many people find this conclusion very unsatisfactory. Some argue that calling altruism selfishness at some other level or in a longer time frame is no way of solving the paradox of altruism. I don't agree; that may just be what it is and there may be no altruism at the level of the genes. Selfishness at the level of the genes can lead to several behavior patterns, including selfishness, cooperation, altruism, or even spite at the level of the individual organism—whichever leads to better selfishness at the level of the genes. Other people argue that at the very least we must stop calling the behavior altruism when we realize that it is a hidden form of selfishness. I don't agree. To us in our day-to-day experience, the individual animal is an obvious entity, and if individuals show altruism it is worth distinguishing it from selfishness at the individual level even if it is selfish at the gene level. Similarly, if animals show altruistic behavior that is reciprocated after a significant time delay, it is worth distinguishing it from routine selfishness. Nothing is gained by labeling everything selfishness. It is only because behaviors recognized as altruistic and apparently paradoxical received so much attention that they engendered in Darwin himself uncertainty about his theory and, later, led to its modification in the form of inclusive fitness theory. Besides, labeling all altruism toward relatives and all reciprocal altruism as selfishness would amount to reserving the term "altruism" for anything that cannot evolve—because we really have no theory to explain altruism if it is not directed toward genetic relatives and if it is not reciprocal, unless of course we uncover genuine examples of the evolution of altruism by group selection.

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Do Animals Favor Their Relatives?

I trust it is obvious by now that terms such as "altruism," "selfishness," and "spite" are routinely used in studies of animal behavior and evolutionary biology for the sake of convenience. They mean approximately what they mean in the human context that we are all familiar with, but they are objectively and precisely defined in terms of the fitness consequences to the actors and recipients. Recall that in Chapter 4 we defined cooperation as an interaction where both the actor and the recipient benefit, selfishness as an interaction where the actor benefits while the recipient suffers, altruism as an interaction where the actor suffers while the recipient benefits, and spite as an interaction where both the actor and the recipient suffer. We have also seen that natural selection is blind to any cost and benefit unless it affects the reproductive fitness of the actors and recipients concerned.

When animals favor close genetic relatives over nonrelatives or distant relatives as recipients of beneficial acts, they are said to be practicing *nepotism.* The use of the term "nepotism" in animal studies does not involve any moral connotation, as it almost always does when applied to humans. When we describe acts of altruism, bravery, or chivalry