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Are Green Beard Genes Outlaws?

Altruistic behaviour is behaviour that causes the recipient to produce more offspring but the altruist to produce less. It can be explained by natural selection if the altruist is more likely to share its gene for altruism with the recipient than with a random member of the population. The problem is how an animal can recognize which other animals in its population share the altruism gene, and which ones do not. Hamilton (1964) realized that genealogically related animals share a greater than random number of genes, so altruism among relatives can be expected to evolve if the recipient gains a sufficiently large number of extra offspring relative to the number lost by the altruist. In the same paper, Hamilton suggested another way in which an altruist could recognize other organisms that possess a gene for altruism. If the genes for altruism also caused their bearers to display some perceptible characteristic, then other bearers of the genes could be recognized directly. Dawkins (1976, page 96) called them 'Green Beard' genes — genes that cause their bearers both to grow a green beard and to behave altruistically towards other green-bearded animals. Natural selection would favour green beard genes if the benefit to the recipient (B) was greater than the cost to the donor (C). So complicated a gene is, as Hamilton stressed, inherently improbable, but that is not the point at issue here.

A gene is an 'outlaw' (Alexander & Borgia 1978) if it will spread against its allele, but if a modifier (a gene at a locus somewhere else in the genome) that totally neutralizes, it will also spread. Genes that bias meiotic segregation are exemplary outlaws (Crow 1979): if they reduce the number of viable gametes, a modifier on another chromosome that restores Mendelian parity will spread. Consider the following numerical example. Suppose an average male typically fathers 50 sons (genotype XY) and 50 daughters (XX). A distorter mutant on the Y chromosome arises which kills all the X-bearing sperm in the male body. This has two consequences: the male's fertility is reduced, but all his progeny will be male and carry the mutant Y chromosome. Suppose that the mutant male produces 70 offspring, all sons, instead of 100 offspring of which 50 are sons. This distorter gene illustrates our definition of an outlaw. It spreads because it produces 70 copies of itself compared to the 50 produced by the non-mutant allele at the same locus. It is also vulnerable to suppression by a modifier on an autosome. Genes on autosomes continue to segregate as normal and so, in an animal bearing the distorter, would produce only $70/2 = 35$ copies. An autosomal modifier which suppressed the effect of the distorter would produce $100/2 = 50$ copies of itself. The modifier would therefore spread because of its relative advantage when sharing a body with the distorter.

It is clear that a modifier that suppresses *part* of the effect of the green beard gene will spread. An animal that retains its green beard but is not altruistic will leave more offspring than the altruistic green-bearded animals. However, from now on we are concerned only with modifiers that neutralize *all* the effects of the green beard gene.

Alexander & Borgia (1978) suggested that green beard genes, which they call 'genetic recognition systems', are outlaws. Thus Alexander (1980, page 113) wrote:

> 'This hypothetical mechanism does not restrict nepotism to relatives by descent; it could operate between any two individuals with the relevant genetic unit in common, and this would increase the likelihood that other genetic units would not be present in the genotypes of both the helper and the helped. Any gene mutating so as to suppress such an 'outlaw' effect by a subgenotypic unit, even partially, would thereby help itself'.

We disagree with this. Genes in the rest of the genome are in exactly the same proportion in the green-bearded helper individuals as in the green-bearded helped individuals. A suppressor modifier would spread if an allele at another locus was less likely to be in a green-bearded helped individual than in a random member of the population, which is simply not true in this case.

The green-bearded animals are only altruistic when it is jointly advantageous: the total reproduction of the altruist and the recipient must be higher than if the altruistic act had not taken place. So all the genes in the green-bearded individuals benefit from the effect of the green beard gene. The crucial point is that if the green beard gene spreads at all it must be advantageous to the whole genome.

The point can be put another way. Imagine a population of green-bearded animals, and imagine that a modifier arose that suppressed all the effects of the green beard gene. Would the modifier be selected for? Individuals containing the modifier would not be altruistic to unrelated individuals, to be sure, but neither would they receive altruism from other green-bearded individuals. Because the green beard gene is only selected for in the first place if $B > C$, the average reproduction of the unmodified green-bearded individuals must be higher than the average reproduction of the modified, selfish individuals. The modifier will not spread. Green beard genes are not outlaws: what is good for a green beard gene is good for all the genes in the genome.

We have discussed the evolution of green beard genes in relation to the alternative of non-altruistic behaviour. This, we believe, is the intention of the idea when it has been discussed before by Hamilton, by Dawkins, and by Alexander & Borgia: it is seen as another way, besides altruism to genealogical relatives, in which altruism could (in principle anyway) evolve. It has been suggested to us that the alternative to altruism among green-bearded animals might be altruism among relatives. Would the green beard gene then be an outlaw? There are two cases, and the answer is no for the first, and yes for the second.

First consider a mutant causing altruism towards other green-bearded individuals irrespective of their genetic relatedness; its allele causes altruism towards relatives irrespective of their green-beardedness. The condition for the spread of the green beard gene is exactly as before: altruism must be dispensed only if $B > C$. Again the gene is not an outlaw.

The second case is where the green beard gene causes extra altruism to green-bearded relatives at the expense of non-green-bearded relatives. This may conveniently be considered for the offspring of the green-bearded mutant. If the mutant is dominant, meiosis produces half offspring with green beards and half without. The green beard gene is supposed to increase the number of surviving green-bearded offspring by decreasing the number of surviving non-green-bearded offspring. This green beard gene is exactly analogous to a 'meiotic drive' mutant and can spread even if it reduces the total number of surviving offspring, provided that it increases the number of surviving green-bearded offspring. If the mutant decreases the total number of offspring but increases the number of copies of itself then it is an outlaw. A modifier that suppressed it and so restored the total number of surviving offspring to its original, higher value would be favoured. Although this has been discussed for the case of the relatives being offspring, in fact it applies for any kind of relative. If the mutant reduces the number of those relatives without green beards while increasing the number of green-bearded relatives then it can spread but, outlaw that it is, it is liable to be suppressed by a modifier.

In summary, a gene that causes its bearer to be altruistic to other animals that bear the same gene when to do so would increase their total number of offspring, is not an outlaw. This is true whether its alternative allele is for not being altruistic, or for being altruistic to other relatives. Only if the gene causes the destruction of those relatives not bearing the gene, to favour those that do bear it, in a manner analogous to meiotic drive, will the gene be liable to neutralization by modifiers.

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