

Outlaw genes with green beards: a response to Ridley and Grafen

Richard D. Alexander

Ridley and Grafen (*Animal Behaviour* 29:954-5) state that they disagree with the statement from my 1979 book *Darwinism and Human Affairs* (p.113) about what I called the “genetic model” of a proximate mechanism for nepotism. This ‘genetic’ model (which Ridley and Grafen call the “green beard gene” following Dawkins (1976), was outlined by Hamilton (1964), and regarded by him as unlikely because it calls for a genetic unit complex enough to (1) have an effect on the phenotype, (2) identify the same effect in other individuals, and (3) respond with altruism appropriate to the situation. I doubted the mechanism on the same grounds and then added:

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 as an ‘outlaw’ effect by a subgenomic unit, even partially, would thereby help itself.

Ridley and Grafen state that “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.” (italics in original). They then state that “However, from now on we are concerned only with modifiers that neutralize *all* effects of the green beard gene.” (italics in original). Next they quote the above passage from my book and then continue: “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.”

In part, Ridley and Grafen have not transmitted my arguments accurately. First, my phrase “such an ‘outlaw’ effect” clearly refers to the tendency to help other individuals solely on the basis of whether or not they have green beards, and not to whether or not a green beard is possessed by the helper, which in itself could not be construed as an ‘outlaw effect’. In the example as given (by me and them), the whole genome could only be helped by the presence of the green beard, without helping tendencies. Thus, Ridley and Grafen have no reason to use my quote in the section of their paper which they say is “concerned only with modifiers that neutralize *all* the effects of the green beard gene.”

In the second part of their argument, by saying that “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,” they apparently mean that “...an allele at another locus...[is not] less likely to be in a green-bearded individual than in a random member of the population...”. Whether or not this is their meaning, I am puzzled by their phrase “exactly the same proportion,” unless they actually mean “on average,” which is not what they say. If “on average” is their meaning, Ridley and Grafen are saying that the gene in the same genome with a green-bearded gene can do no better than to go along with its tendency to treat other individuals as if they were 100% like it genetically if they possess green beards, while the rest of the genes in the genome have only a random or slightly higher chance of being in the helped individual.

I think I understand how they came to this argument—i.e., from the assumption that it would be useful to all genes in the genome to have their bearer help anyone who has even a slightly higher than random chance of carrying any gene in the genome. This would only be true, however, (1) if a random or slightly higher than random likelihood of being in the helped individual’s genome is sufficient to cause the helping to improve the reproduction of the modifier gene, and (2) if no better alternatives exist. Ridley and Grafen do not mention either of these points, but say that “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” (italics added). The meaning of this statement

is unclear to me, since a suppressor's spread would depend on its own likelihood of being in helped individuals.

This part of Ridley and Grafen's argument does not seem very important to me. It seems reasonable to carry on the discussion only if three assumptions are being made: (1) that individuals in this species have a certain ability to help others socially, (2) that the help improves the reproduction of the helped, and (3) that the amount of help that can be given is finite. Given these assumptions, what will determine how selection works on genes modifying "green beard" genes' tendencies to help will be what alternatives exist for use of the help. Green beard genes may be expected to cause their bearers to treat other individuals with green beards as if they were like themselves, since every green-bearded individual carries the gene leading to green beards. It is difficult to believe that there could be a species in which *this amount* of help would not be contrary to the interests of other genes in the genome, whether randomly, less than randomly, or slightly more than randomly likely to be present in the helped green-bearded individual. It is the *disparity* between the interests of the green beard gene and those of the rest of the genes that makes its helping choices and degrees of effort an 'outlaw' effect. And it is the difference between this "genetic mechanism" and that of "acceptance or rejection of a particular *class* of relative by comparing phenotypes," which can be learned, that I wished to stress in *Darwinism and Human Affairs*.

Edited by D. Lahti, 9/5/21