

Reflection Questions on Chapters 2 & 3

First, let's recap some of the ideas and questions that arose last week. Chapter 1 of *The Selfish Gene* defined biological altruism in fairly precise terms as any "behaviour" that promotes the fitness of some non-related organism while reducing the fitness of the individual who performs that behaviour. A few points of clarification apply just to this definition:

- Technically, biological altruism is not restricted to behavioural traits. Any trait that "reduces" the fitness of its bearer, while benefiting the fitness of some unrelated individual, qualifies as biologically altruistic. Consider the trait of growth rate in some species of oak tree. Let's assume that increased growth rate provides a competitive advantage because faster growing oak trees tend to gain more access to sunlight. A tree that has a reduced growth rate, in relation to some unrelated individual, would qualify as biologically altruistic.
- What, you might ask, do we mean here by "unrelated"? After all, every living thing on earth shares a common ancestor. Aren't we all related then? This is a bit of a tricky issue. Most advocates of gene-centric thinking define relatedness in comparison to the average degree of relatedness in some population. If we consider a population of oak trees, there will be a large number of genes that they all share in common. But there will also be a certain amount of genetic variation among those oaks. When thinking about relatedness among members of the same species, we are just talking about those genes (those alleles, to be precise) that vary. In any such population there will be an average degree of "relatedness" among any two randomly chosen individuals. If two particular trees, A and B, share more alleles with one another than average, then they are "related". But if tree A and C share an average number of alleles, then they are "unrelated."
- Let me also say a word about this idea of "increasing" or "decreasing" the fitness of an unrelated individual. This way of speaking might have struck some of you as a little strange. Consider a particular oak tree. It emerges from a fertilized seed at a particular location in the forest floor. There will be no modifications to its genome over its lifetime. Also, at the point that the seed is established its environmental context is pre-determined. There are going to be certain other trees that will exist in its vicinity over the course of its life. There will be a certain number of days of sunlight, of rain, etc. So, if its genetic background is fixed at "birth," and if the environmental factors that impact its reproduction and survival are likewise set in stone, what on earth could it mean for some other tree to come along and "raise" or "lower" its fitness? To put the question differently: let's assume that each genotype corresponds with a particular expected number of offspring given a particular environment. This expected reproductive value is the fitness of that genotype. What on earth could it mean for that value to be raised or lowered? It isn't as if the expected reproductive value of an organism is going up and down from one moment to the next.

I think that the best way to deal with this issue is by understanding "increasing" and "decreasing" in a contrastive sense. For example, consider a particular trait (growth rate R) that

is possessed by some organism (A). Now take the statement, "R decreases the fitness of A, while increasing the fitness of some unrelated individual B." What this must mean is the following:

- compared to some actual or hypothetical individual (call it D), that is identical to A in every relevant respect except that D lacks the trait in question (growth rate R), then
- A is expected to have fewer offspring than D,
- and, C is expected to have more offspring the company of A than it would in the company of D.

This seems like an acceptable notion, provided that the hypothetical or actual individual (D in this case) is some genotype that we can reasonably expect to appear in the population that we are talking about. I mention all of this just so that we are clear what this short hand way of talking (increasing vs decreasing fitness) actually means.

- Another topic that came up last week was this thorny issue of reciprocal altruism. Let me first explain that is a technical term with a specific meaning. Once we understand that meaning, we realize that this term is actually quite misleading, since reciprocal altruism isn't actually a form of biological altruism. It is actually a form of biological selfishness.

Reciprocal altruism was posited as an explanation for cooperative behaviour by a very influential gene-centric thinker named Robert Trivers. We can think of it as a type of evolutionary process, where organism A "increases" the fitness of some unrelated organism B, on the condition that B makes a similar "contribution" to A's fitness at some later point in time. This is a form of biological selfishness because A is not taking a reduction in its fitness if we consider things from the perspective of an evolutionary time scale. If B enhances A's fitness, over the long term, as often as A enhances B's fitness, then the two genotypes can have a stable co-existence in some population over indefinitely many generations.

Now, I don't have a conceptual difficulty with this idea. But I do want to draw attention to some potential issues surrounding this idea. First, as a hypothesis to explain cooperative behaviour, reciprocal altruism is very difficult to falsify. The idea presupposes some way of doing the accounting of fitness contributions across time. In practice, this is very difficult if not impossible. It becomes particularly challenging if we allow that the fitness "donations" can occur over successive generations. For example, A might "increase" the fitness of B by reducing its growth rate. But A itself might not receive a reciprocal contribution in its lifetime. This might not come about until the next generation, when B's offspring interact with A's offspring. From a scientific perspective, these interactions are very difficult to track. So, if one fails to find a reciprocal relationship among two organisms, it is always an option for the gene-centric thinker to argue that we have not looked hard enough. Reciprocal altruism (and by extension, gene centrism) is very difficult to falsify for this reason.

- A final topic that arose during our last meeting concerns the meaning of group selection. Dawkins defines it simply as the "reduction" of an individual's fitness in some way that benefits "the group or the species." This description is inexcusably sloppy for at least two reasons. First, he is conflating the differential survival and reproduction of groups with the differential survival

and reproduction of species – as if they were effectively the same process. But it should be clear that group survival and reproduction is a very different sort of process from species survival and reproduction. A group is a collection of organisms that interact with one another in some way that sets them apart from other groups. We tend to think of groups as spatially segregated, if only for a stage of their life cycle. Group survival involves the continuity or re-emergence of a particular set of individuals or their offspring over successive generations. Group reproduction involves one group “budding off” into other groups. By contrast, species are organisms that are capable of reproducing (setting aside asexual species for now). It is difficult to say what it means for a species to persist, because they can change over time. We tend to think that homo erectus is a different species from homo sapiens, even though they are different stages of a single lineage. Species “reproduction” is speciation. This can occur whenever a single species becomes separated by a geographic barrier, and eventually acquires enough mutations to prevent interbreeding.

It should be clear that these are two very different processes. A species is not something that can easily form, disband, and reform over successive generations. Nor is it common for members of a species to huddle together and “exclude” other species. In fact I don’t even know what that would mean. However, these are properties that one commonly finds in groups. Another important difference is that speciation is inevitably a slow process since it involves the accumulation of many mutations. We can assume that many generations are required in order for speciation to occur. By contrast, a group can “reproduce” by budding in a relatively short period of time.

Now, I actually think that it is intellectually dishonest for Dawkins to equate these two different levels of selection. Species selection is indeed “weak” force compared to individual-level selection, largely because it is so slow. But this isn’t necessarily the case for group selection. It seems that by lumping these processes together, Dawkins is presupposing the very thesis that he hopes to defend: that selection really only acts at the level of the individual/gene.

I have another issue with Dawkins’ description, namely that he doesn’t actually describe the process of group selection. Instead, he defines group selection in terms of an outcome, that is, in terms of an altruistic trait. In order to think clearly about these issues, we need to realize that group selection is essentially the same process as gene-level or individual-level selection, only that it is “bumped up” to the level of the group. Selection (at any level) involves three components: phenotypic variation in some focal entity that is heritable and which impacts fitness (survival and reproduction). Simple as that.

I think that Dawkins’ definition is an attempt to stack the deck in favour of gene centrism. He defines group selection as a decrease in fitness, but tells us nothing about how such a decrease plays out at the group level. When stated so vaguely, we are naturally led to conclude that group selection could not work. By definition, selection favours traits according to their fitness. The problem, put slightly differently, is that Dawkins doesn’t even acknowledge that group selection requires fitness differences among groups *in addition to* within groups. That is, he seems to assume that selection only acts within the group in order to argue that selection acts only within groups. This is a classic example of the philosophical fallacy begging the question – assuming the very thing that one aims to conclude.

Questions for Jan 24. Please submit by 1:00 pm using Dropbox

- 1) In Chapter 2, Dawkins proposes that “stability” is a fundamental property that is at the heart of all biological systems. According to his story, life began with the emergence of an entity that managed to achieve a sort of stability through copying. Everything else that has happened in biology (such as the evolution of organisms) can be understood as an attempt to preserve stability of the replicator.

This view of biology is potentially challenged by the idea of evolvability. This is the idea that organisms (not genes) sometimes increase their mutation rate in order to adapt, for example, to a variable environment. Dawkins attempts to deal with this challenge at the bottom of page 22 (in my copy), in the paragraph that starts with, “If you already know something about evolution, you may find something slightly paradoxical about the last point.” In a short paragraph, using your own words, explain what is Dawkins’ response to the challenge of evolvability?

- 2) Early on in Chapter 3, Dawkins distinguishes his definition of a gene from the conventional idea of a cistron. Explain this distinction in your own words. Make sure to explain why Dawkins thinks that most cistrons are not genes.
- 3) A little further in Chapter 3, Dawkins uses his definition of a gene to develop an argument for why selection can only act at the level of the gene (not on individual organisms or on groups of individuals). The argument is at the bottom of page 43 in my edition, and begins with the sentence, “In sexually reproducing species, the individual is too large and too temporary a genetic unit to qualify as a significant unit of natural selection.” In your answer, outline Dawkins’ argument here and briefly comment on its strengths and/or weaknesses.
- 4) One might reasonably argue that Dawkins theory, if we were to take it seriously, cannot explain the existence of individual organisms. In an organism we see a high degree of cooperation among genes. Only in special cases do certain genes “take advantage” of the other genes, for example, by reproducing more rapidly than the collective. Yet, we know that genes have the capacity to behave really selfishly. One example is the contagious form of facial cancer found in Tasmanian devils. More common examples include meiotic drive and transposable elements. So, why do the genes in an organism usually cooperate, if selection acts exclusively at the level of the gene?

Dawkins’ attempt to answer this question comes at the end of Chapter 3 with his analogy oarsmen. In your own words, explain how this analogy is supposed to work. We can discuss its plausibility in class.