

Kin Selection Theory is Wrong

Blithering Genius

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1 Introduction

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. – Richard Dawkins, *The Selfish Gene*, Chapter 6

Challenge accepted. And I will use Dawkins’ own concept of the extended phenotype to do it.

In this essay, I will explain how parental altruism is selected for, without any assumption of kin altruism. In other words, I will explain that selection is based on reproductive fitness (the ability to reproduce), not on inclusive fitness.

2 Lack of Evidence of Kin Altruism in Nature

First, we do not see strong evidence of genetic altruism in nature. Organisms do not act altruistically toward one another based on either genetic similarity or degree of relatedness.

This can be observed within any family. Parents are much nicer to children than children are to parents. Human children reward parents psychologically with smiles and little gifts, but human parents put in hours of work every day to take care of their children. Parents are also much nicer to children than siblings are to each other.

There is some sibling altruism in nature, but also a lot of sibling rivalry. In general, the relationship between siblings seems to be more competitive than altruistic. If organisms acted to perpetuate their genes regardless of which body those genes were in, siblings would treat each other about as nicely as parents treat children. That is clearly not the case for most species.

See Does Evolutionary Theory Imply Genetic Tribalism?.

There are some species with behaviors that look like kin altruism. There are the so-called “social insects”, such as bees and ants, in which children act altruistically toward the parent and toward each other (sort of). There are the often-mentioned alarm calls of ground squirrels. There are probably a few other examples that are commonly used to illustrate the claims of kin selection theory. In what follows, I will provide an alternative explanation for those behaviors.

Before getting into the details of why kin selection theory is wrong, I want to call attention to the unscientific nature of it. The theory was constructed to explain a small number of examples, at the expense of making a much larger amount of data harder to explain.

3 Kin Selection Theory Has No Explanatory Power

Sibling rivalry and sibling indifference are much more common than sibling altruism, and yet kin selection theory predicts the latter, while making the former harder to explain. Instead of fitting the theory to the data, the proponents of kin selection theory cherry-pick data to fit their theory. They treat any example of apparent altruism between kin as evidence for their theory, but do not consider examples of competition between kin, such as siblings killing each other, as evidence against their theory. This is an inductive fallacy.

Clearly the proponents of kin selection theory are motivated by something other than truth-seeking. They are not evaluating the theory in terms of its explanatory power.

So, the first criticism of kin selection theory is that it has no explanatory power. In fact, it has negative explanatory power. It makes the data harder to explain, not easier.

4 Reproduction is about Copying the Phenotype, Not Genes

Now I'll give my response to Dawkins' challenge. I will explain why natural selection produces parental altruism, but not (in most cases) altruism toward collateral kin. I will also explain those rare exceptions of apparent kin altruism, such as the bees. After doing that, I'll debunk the guts of kin selection theory: Hamilton's rule.

Life forms are selected to reproduce. Reproduction is just the creation of new organisms from existing ones. It has no higher purpose or telos. Organisms do not reproduce in order to increase the frequency of their genes. They reproduce because their forms were selected to reproduce.

Reproduction is not just about copying genes. Reproduction is about copying the phenotype. It is the creation of a new reproducing machine, not just the creation of copies of DNA sequences.

Reproduction is not just the creation of offspring. The offspring must be capable of reproducing themselves. An organism that produced millions of sterile offspring would cease to exist after two generations. Reproduction is a cycle, and it is only complete when children reproduce.

5 Children, Parents, and the Extended Phenotype

Parental altruism improves reproductive fitness, because it enables offspring to survive and reproduce. All parents are altruistic to some extent. The minimal amount of parental altruism is the creation of a gamete. In many species, parents provide other benefits to their offspring, such as protecting them, feeding them, and teaching them. Such behaviors can evolve if they increase the reproductive fitness of the parents. They are energetically altruistic, but not reproductively altruistic. Parental altruism is reproductively selfish.

Conversely, children are not usually altruistic toward their parents, because investing energy in parents is not a good reproductive strategy. For the child, being altruistic to a parent or sibling would be a waste of energy, because the child cannot reproduce via the parent or sibling. Parents and siblings are related to the child, and they have genes in common, but reproduction is the basis of natural selection, not shared genes or relatedness. So, organisms typically invest in having offspring of their own, rather than helping parents or siblings.

If selection is based on reproductive fitness, then we would expect parental altruism to be common, and other types of altruism to be non-existent, or require some additional explanation. When we look at nature, we see that parental altruism is common, and other types of altruism appear to be rare. But what about those apparent cases of sibling or kin altruism, such as the bees, ants and alarm-calling squirrels? Can their behavior be explained in terms of reproductive fitness?

Yes. Sibling altruism can evolve because *the child is part of the extended phenotype of the parent*. A trait can be positively selected because it confers a reproductive advantage to the parent when it is expressed in a child.

5.1 The “Siblicide Gene” Thought Experiment

Suppose that an organism has a “siblicide gene” that causes it to kill its siblings. This behavior could be adaptive. The sibling killer gets more parental resources, and is thus better able to survive childhood and have offspring of its own. However, the siblicide gene becomes maladaptive once it is expressed in the killer’s offspring. Individuals without the siblicide gene have an advantage when they become parents themselves, because their offspring are less likely to kill each other.

This explains why sibling rivalry is typically milder than you would expect from reproductively selfish individuals. It also explains how sibling altruism can evolve: because it improves the reproductive fitness of the parents.

When siblings are altruistic toward one another, they are acting as part of the extended phenotype of their parents. Their actions help their parents to reproduce. The parent’s genes are not only

expressed in the parent, but also in the child, and so genes can be selected for inter-generational effects.

5.2 Species and Parental Care

In most species with parental care, siblings tolerate each other, but do not actively help each other. Only in very unusual cases, such as bees and ants, do children sacrifice themselves for the sake of their siblings and/or parents. Bees and ants are a special and extreme case of inter-generational selection. (See Bees are not Social for a detailed explanation of bee behavior.)

Among species with parental care, there are some in which children are often killed by siblings or even by parents. In some bird species, the parents brood two eggs, but may throw one chick out of the nest if both hatch. They will typically throw the weaker one out of the nest, after observing the competition between their offspring. It's a cruel but effective reproductive strategy. Laying two eggs reduces the risk of having no offspring that season. Killing the weaker chick allows the parents to invest more in the remaining chick. Even parental altruism has its exceptions.

5.3 Hypothetical Inter-Generational Selection

It is possible that a species could evolve altruism toward more distant relatives, such as cousins, but that would require special conditions, such as a multi-generational hive. In a sense, the body is a multi-generational hive, and the somatic cells are part of the extended phenotype of the zygote. (See Sex, Death and Complexity.) Beehives and bodies are reproductive units. Their constituent members are selected to contribute to the reproduction of the whole. That is not true for a species, subspecies or society. Inter-generational selection cannot create altruism at the level of a species or subspecies, and it has nothing to do with human social organization.

What we see in nature fits the theory that selection is based on reproductive fitness, not inclusive fitness. Both parental altruism and sibling altruism are better explained by this theory than by kin selection theory.

6 Debunking Hamilton's Rule

6.1 Defining Hamilton's Rule

Now to debunk the guts of kin selection theory, Hamilton's Rule. Here is the definition from Wikipedia (source):

Formally, genes should increase in frequency when

$$rB > C$$

where

r = the genetic relatedness of the recipient to the actor, often defined as the probability that a gene picked randomly from each at the same locus is identical by descent.

B = the additional reproductive benefit gained by the recipient of the altruistic act,

C = the reproductive cost to the individual performing the act.

This seems plausible enough. If a gene causes an altruistic behavior, that behavior will be selected for if it benefits other carriers of the gene (on average) more than it harms the altruist, and that will be the case if $rB > C$, right?

No. There are huge errors in the reasoning above.

6.2 Relatedness Between Relatives

One false assumption is that r (genetic relatedness) will give you the probability that the altruistic trait/gene is present in the beneficiary of the act, or at least a lower bound on that probability. This seems plausible at first glance, because relatedness measures the probability of a random gene being identical by descent. For example, the probability that two siblings inherit a specific sequence of DNA from the same parental sequence is 50%, and thus for siblings $r = 0.5$. So, what is the fallacy?

Traits aren't random, especially maladaptive ones.

Here's a little thought experiment to illustrate this. Suppose that a mother duck has eight babies with the same father, and let's suppose that half of those ducklings have inherited an altruistic trait. The altruistic ducklings will try to defend their siblings from predators. The selfish ducklings will swim away from trouble with no regard for the others. Let's suppose that $rB > C$, so according to Hamilton's rule this trait should be selected for. The ducklings are related by 0.5, so $rB > C$ means that the aggregate benefit (decreased risk of death) to the other babies is more than twice the cost (increased risk of death) to the defenders.

Initially, half of the babies have the gene for the altruistic trait. However, the altruistic ducklings are more likely to be killed by predators than the selfish ducklings, so over time the percentage of altruistic ducklings declines relative to selfish ones. Suppose that two of the altruists sacrifice their lives to save their siblings from predators. Now there are two altruistic ducklings and four selfish ones. The survivors still have a relatedness of 0.5, but the probability of helping a fellow altruist is now 0.2 (one in five, since there are five other ducklings that an altruist could help, and only one is a fellow altruist).

Hamilton's rule does not define the selective pressure on the altruistic trait, because r is not a lower bound on the probability that the beneficiary has the same trait. The reason is selection. Ironically, Hamilton's rule ignores the effects of selection.

The same fallacy occurs in claims of altruism at the level of species, race or ethnic group. Some people have theorized that populations with high relatedness (so-called "clannish" populations) can evolve altruistic behaviors, because the recipients of such behaviors are likely to have the same trait. Again, this ignores the effect of selection on the probability of the recipient having the same trait. You can't assume that gene/trait probabilities are fixed when you're reasoning about selection, unless you want to be completely illogical. Altruism within a population P might increase the size of P relative to other populations, but it would still select against the altruism trait itself.

6.3 Hamilton's Rule and the Free Rider Problem

Hamilton's rule ignores the effect on non-altruists. Suppose that Hamilton's rule applies to a population with a high degree of relatedness, so that $rB > C$ for some altruistic trait. In that case, the trait confers a reproductive benefit on itself, at least initially. However, if the population contains selfish individuals, then those individuals will receive the same benefit without paying the cost. Thus,

the selfish trait will increase relative to the altruistic trait, regardless of whether the frequency of either trait goes up or down. And as the selfish trait increases relative to the altruistic trait, selfish individuals will receive more and more of the benefits of altruism.

Basically, reproductive altruism can't evolve because of the free rider problem. An environment of altruists is a great environment for a selfish variant, and so the selfish variants will be selected for, gradually reducing the percentage of altruists in the population, until most of the benefits of altruism are received by selfish individuals. Reproductive selfishness is the only thing that can evolve (at least without artificial selection).

6.4 The Problems with the Green Beard Mechanism

The "green beard" mechanism has been proposed as a possible solution to this genetic problem of cooperation. It involves a gene with two phenotypic effects: (1) a visible trait (such as a green beard) and (2) an altruistic behavior toward other individuals with the visible trait. This is not plausible because (a) it's very unlikely that a gene could produce such a complex phenotypic effect (it's a Rube Goldberg machine), and (b) there is a simple counter-strategy: grow the green beard but suppress the altruistic effect.

There is no need for convoluted hypothetical mechanisms to explain reproductive altruism, because there is no reproductive altruism to explain. The efforts to fit altruism into evolutionary theory are not about explanation. They are attempts to protect quasi-religious beliefs from the implications of evolutionary theory. Hence the mental gymnastics and blatant violations of Occam's razor. (See Evolution and Morality.)

6.5 Selective Forces Don't Necessarily Increase the Frequency of Genes

There is another problem with the version of Hamilton's rule given above: it uses the wording "genes will increase in frequency" instead of "a gene/trait will be selected for" or "a gene/trait will be adaptive". Even if Hamilton's rule defined the selective pressure on a gene/trait, that wording would be incorrect. Positive selection is not necessarily an increase in the frequency of a trait or gene. Maybe that's just a mistake in the wording on Wikipedia, but it's worth pointing out.

Selective forces do not necessarily, or in most actual cases, increase the frequency of genes. Most of the time, selection acts in an equilibrium state to maintain that equilibrium. It is wrong to think of selection as a matter of increasing or decreasing the frequency of a single gene or trait in isolation. Selection is about the relative proportions of competing genes/traits, and selection pushes a population toward an equilibrium state in which competing genes or traits are equally fit.

7 Conclusion

Let's wrap this up. To summarize:

- There is very little evidence of kin altruism in nature, other than parental care of offspring and sibling tolerance.
- The child is part of the extended phenotype of its parents, and thus child behavior can be selected to increase parental reproductive fitness.

- The relatedness term (r) in Hamilton's rule is not a lower bound on the probability of sharing a trait, because of selection (altruism has a cost).
- Even if Hamilton's rule applies to a population initially, the free rider problem will reduce the probability of the benefits of altruism going to a carrier of the altruistic trait and increase the probability that the benefits go to a non-carrier.

Thus, kin selection theory is wrong.