Selfish Gene Confusion

By Michael White | July 10th 2009 05:08 PM | 11 comments | Print | E-mail | Track Comments

In light of the popularity of this piece, here are some things to keep in mind about 'selfish' genes:

1. The basic issue is about the unit of selection – does natural selection choose allele, individuals, populations, or species? The answer, like most things in biology, is yes, as Douglas Futuyma puts it in his standard textbook on evolution (p. 354. 3rd edition):

> *If, then, our concept of levels of selection includes causality, natural selection can act at the level of the gene (as in meiotic drive), organism, and at least in principle, population and species.*

Futuyma lays out the general view of group (which can mean species or population) selection (p. 351-352):

> *No one denies that group selection, if sufficiently intense, might prevail...[in fact, it has been demonstrated to be possible by experiment] but many, perhaps most, evolutionary biologists believe that it is only rarely an important force in evolution.*

2. When it comes down to genic selection vs. individual selection, the issue is more a matter of useful perspective. There is so much diversity in biology, and some situations are more usefully considered from a gene's eye perspective, while other's aren't. There are no absolute laws of selfishness here. There are clear examples of genic selection, that can't be explained by the advantage an allele confers on an individual. These are classic selfish elements, as Futuyma notes:

> *An increase in the frequency of a "selfish" genetic element, such as a t allele in the mourse or Medea in flour beetles, is evidently due to* ***genic selection****: selection of an allele because of its capacity for distorting segregation, irrespective of its effect on the organism that bears it. But if an allele increases in frequency because it enhances the organism's survival or fecundity, shall we call that genic selection or individual selection? Again, opinions differ.*

Ford Doolittle and Carmen Sapienza, in a classic piece on selfish genes in the April 17, 1980 issue of *Nature* make the same point:

> *If there are ways in which mutation can increase the probability of survival within cells without effect on organismal phenotype, then sequences whose only 'function' is self-preservation will inevitably arise and be maintained by what we call 'non-phenotypic selection'. Furthermore, if it can be shown that a given gene (region of DNA) or class of genes (regions) has evolved a strategy which increases its probability of survival within cells, then no additional (phenotypic) explanation for its origin or continues existence is required.*

Leslie Orgel and Francis Crick made the same point in the same issue of *Nature*, comparing selfish DNA to parasites:

> *In the case of selfish DNA, the sequence which spreads makes no contribution to the phenotype of the organism, except insofar as it is a slight burden to the cell that contains it... The spread of selfish DNA sequences within the genome can be compared to the spread of a not-too-harmful parasite within its host.*

Experience has shown that these ideas are right: our genomes are filled with parasitic, virus-like pieces of DNA that, for the most part, make no phenotypic contribution. (Actually, their potentially negative phenotypic consequences are kept to a minimum by active surveillance and suppression.)

Bottom line: there are clear examples of 'selfish' genetic elements, with no positive fitness contribution, and which exist simply by virtue of the fact that they can perpetuate themselves.

3. Now what about 'regular genes' - the ones that contribute positively to our phenotype? Should we consider them 'selfish'? Selfish is actually a distracting term (as Dawkins himself has said). Again, the real issue, as both Futuyma and Dawkins point out, is at what level selection operates - allele or individual.

Obviously, the fitness effect of any given allele depends on its context - the other alleles around it in the genome. An allele in say, a myglobin gene, with the potential to make a faster-running cheetah, is useless if that allele is coupled with an allele that causes blindness. That's an extreme example, but the basic point is true: the effect of most alleles depends, more or less, on context.

From a gene's eye view however, it's not so necessary to consider context in order to make useful predictions about the evolutionary future of a gene: you can simply calculate the average fitness contribution of an allele, over all genetic backgrounds, and predict the evolutionary consequences. As Futuyma summarizes Dawkins' ideas about selfish genes,

> *Natural selection within population can be understood simply as a competition among alleles, the winner being the one that confers some characteristic on organisms that provides that allele with the highest rate of survival and reproduction, averaged over all the gene combinations in which that allele occurs.*

This perspective works well in some cases, but the gene's-eye view doesn't work as well in other cases

– such as the phenomenon of overdominance. The classic case is the sickle-cell allele and malaria resistance. In this case, people who are heterozygotes, carrying one normal beta-hemoglobin allele and one sickle cell allele, are more resistant to malaria than people with two normal beta-hemoglobin alleles. This means that, in one particular combination, a normally harmful allele (the sickle cell allele) has a beneficial effect. But averaged over all combinations, the sickle-cell allele is harmful. Overdominance is not a situation that is not easily predicted from a gene's-eye perspective.

On the other hand, overdominance seems to be rare. And we're again reduced to noting that biology is so diverse, that in some cases one approach is fruitful, while in another case, we should use a different perspective.

4. The most controversial aspect of Dawkins' selfish gene argument is related to altruism. Dawkins lays it out in the introduction to the 30th anniversary edition of *The Selfish Gene*:

> *We should not be surprised to find individual organisms behaving altruistically 'for the good of the genes', for example by feeding and protecting kin who are likely to share copies of the same genes. Such kin altruism is only one way in which gene selfishness can translate itself into individual altruism...*

I'm going to sound like a broken record: it depends. There are many, many clear cases of kin selection, and calculations of altruism based on genetic relationships, like this one:

> *In eusocial Hymenoptera such as ants, wasps, and bees, diploid females develop from fertilized eggs and haploid males from unfertilized eggs. As a result, queens are equally related to their sons and daughters, whereas workers are more related to their sisters than to their brothers. These asymmetries in relatedness suggest that queens should favor an equal investment in both sexes, whereas workers should favor greater investment in females than in males. Hence, a sex ratio conflict arises between queens and workers, because workers may enhance their inclusive fitness by altering colony sex ratios in their favor, and in so doing act against the interests of the queen. The resolution of such conflicts provides important insights into the role of kin selection in social evolution.*

The conclusion of this paper: kin selection happens.

> *By eliminating males, workers preferentially raise the sex that yields the largest marginal fitness-return per unit investment, thereby enhancing their inclusive fitness. This implies accurate discriminatory abilities at two stages: First, accurate assessment of queen mating frequency, which suggests great diversity of genetically determined odor cues. Second, discrimination between male and female brood relatively early in development, before males are so large that it would be too costly to kill them. These findings emphasize the sophistication both of worker reproductive strategies and the recognition abilities on which they often depend. More generally, they illuminate some of the complex dynamics between cooperation and ongoing conflicts among members of insect societies.*

Kin selection has be extremely successful at predicting the social dynamics of many animal social behaviors – in birds, mammals, reptiles, amphibians, and insects. (Futuyma goes over a long list in his textbook, p. 597-599). Biologists have tested the theory with experimental populations, and with natural experiments. In case after case, we can explain cooperative behavior in the animal world by calculating genetic relatedness.

Calculating relatedness and making predictions isn't the same thing as finding a gene that influence altruism. Now researchers are starting to find those genes. In a paper in last year's *Genetics*, researchers identified regions of DNA that control worker bee behavior. In the honeybee species *Apis mellifera*, female workers give up their chance to reproduce by not laying eggs. Reproduction is left to

the queen. This behavior is what kin selection predicts, but what genes are involved? Can we find 'cheater' mutants that cause female workers to go ahead an lay eggs?

As the authors write:

> *In societies where individuals act to benefit other members of the society at a cost to their own direct fitness, there is a selective advantage for individuals that "cheat," reaping the benefits of group living while avoiding the cost of contributing personally. Where genes influence cooperation among individuals, single mutations at key loci may permit selfish behavior to arise that advantages the carrier, but reduces the fitness of the group. Thus, identifying mutations for cheating behavior provides the opportunity to characterize the genetic architecture of cooperation—a key goal of sociogenomics.*

Such cheater strains of bees exist, called 'anarchist lines'. By crossing anarchist males with normal queens, the researchers were able to find an 'anarchy locus' that influences altruistic behavior.

So what we have is this: a theory (kin selection) that predicts that, in many cases, natural selection will favor altruistic behavior towards kin, and we have a definite locus that does in fact confer altruistic behavior – a region of DNA that contains a variant of a gene that causes female workers to cease laying eggs in the presence of a fecund queen.

Kin selection is a powerful theory.

But biology is not like physics, and kin selection is not an absolute law – there are clear cases where other factors can take precedence of genetic relatedness, most notably cultural pressures in human societies (although clearly relatedness has an influence on altruism even among humans).

The main lesson here is that, under the heading of 'selfish genes', we can find some exteremely powerful ideas that have found substantial support in the lab and in the field. Whether or not the term 'selfish' is the best one to use (and Dawkins' has expressed ambivalence about the term, and the everyday connation of the term has little relevance to the actual, rigorously developed scientific ideas), thinking about evolution from the perspective of alleles is extremely useful.

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COMMENTS

Hi,

I'm an evolutionary biologist at Oxford interested in social evolution. I've started a blog (http://elmouden.blogspot.com/) and my first entry is on the selfish gene. There is lots of confusion about the meaning of "selfish gene" in the social science literature. The fact that copies of genes can lead to altruistic, spiteful, mutual or selfish behaviour and the fact that genes maximise their fitness (which is what Dawkins described as selfish) are two separate concepts (but confusingly with an overlap of terminology).

Hope to talk more
Claire

Link **Claire El Mouden** (not verified) | 07/10/09 | 18:05 PM

Thanks for the link to your new blog. I'm interested in seeing more there from the social science side of this issue – my realm is obviously in genetics, not social science. Good luck with the blog.
—
Mike

Link **Michael White** | 07/10/09 | 21:28 PM

While not specifically on the selfish gene issue, questions on levels of causation within evolution have been a "hot" issue the last few years in the journal *Philosophy of Science* -- whose academic focus is presumably obvious ...

I could drill down into the archives if you need, but if you've ready access to a University Library you'll probably be better situated to do a search of the term "selection" for that journal.

Link **Gary Herstein** | 07/10/09 | 21:41 PM

Mike, you said this in a comment to "that piece".
There is no such thing as a 'fundamental law of gene selfishness'
That's just disingenuous.
An entire thought system and dogmatic view of the workings of evolution has been based on the assumption that there is such a fundamental law.
You are attempting the impossible. You're trying to defend the thought system after conceding that it's basis does not exist.

Link **Steve Davis** | 07/10/09 | 18:06 PM

You keep saying that, but you never actually show it. You only speak in vague generalities; you never dive into the actual research literature to prove your case.
—
Mike

Link **Michael White** | 07/10/09 | 20:58 PM

Now I'm going to sound like a broken record. What you're describing is "self-interest" where selfishness and altruism represent two states than an encounter can produce.

My insistence is not semantic, but rather to bring the dialog into line with game theory and other methods for making predictions. As you know, in game theory we have cooperators and defectors. How logical does it sound to start a dialog about the Prisoner's Dilemma and say that we're going to model the encounter of two defectors (and then conclude that they cooperate)?

> *Experience has shown that these ideas are right: our genomes are filled with parasitic, virus-like pieces of DNA that, for the most part, make no phenotypic contribution.*

Which is exactly what one would expect from genes acting in their own "self-interest" with no "concern" about replication. In other words, any development (as long as it isn't harmful) is simply carried along by the tide. Assigning any intent more significant than that is simply not warranted.

Selfishness isn't simply a social term, it is a term that describes the outcome of an encounter with another entity. The development of the genes is NOT selfish, but in the vast majority of cases concludes with them doing what they do (self-interest) and in most encounters, they behave cooperatively or indifferently.

> *In case after case, we can explain cooperative behavior in the animal world by calculating genetic relatedness.*

But is this true or merely coincidence, since the vast majority of encounters will be confined geographically and thus lead to the likelihood that offspring will more frequently be in the same general vicinity as other related animals. A recent experiment suggests that it is familiarity and not kin that plays the major role (Kin recognition versus familiarity in a solitary mustelid)

As near as I can find, there have been few actual experiments to confirm kin other than the higher probability that animals in the same geographic area will be related (which is the same phenomenon we see in humans - children raised together will tend to view each other as siblings even if they are unrelated).

As for Dawkins, he's made it quite clear when he refers to organisms as "throwaway survival machines" that he's not ambivalent about the term selfish at all.

> *"We animals exist for their preservation and are nothing more than their throwaway survival machines"*

In addition, I'm not sure that the introduction of eusocial insects is warranted as a selective choice for "altruism", since they behave no more altruistically than the cells that make up your body. This is one reason why ant and bee colonies are considered "superorganisms" because they represent a multi-level organism in the same degree that multicellular organisms different from single-celled ones.

I agree that there is much diversity in biology and it's very difficult to come up with singular laws that describe what's taking place. This is precisely why I'm so insistent that the wrong terms are worse than no terms at all. If they cannot be used to describe something resembling a "law" then they shouldn't be used in that fashion.

Despite the denials that "selfish" is just a metaphor, or that it's simply a semantic argument, the evidence suggests that it is anything but, when the explanation given is how they truly do behave selfishly.

As I've stated elsewhere, the genes create the organism, which is subject to sexual selection for reproductive purposes. There are some genes that will represent highly conserved processes which we would expect to see propagated with a high degree of replication, while others may be less so, with a fair number being carried along that contribute nothing at all.

Reverting to the computer analogy, the argument about genes, is tantamount to saying that the operating system's success is dependent on a particular interrupt handler, or a particular application. In truth, the useful elements will be carried forward between releases, while others will change to improve functionality (and yes there is even some code that may not do anything useful anymore, but it's easier to keep than to remove it). It makes no sense to consider the operating system except within the context of all of it's parts (regardless of the degree to which any one contributes), just as is the case with organisms. They are the totality of their genes and their survival depends on the aggregate and not the singular.

—
Mundus vult decipi

Link **Gerhard Adam** | 07/10/09 | 18:53 PM

> *My insistence is not semantic*

But that's what all of your comments revolve around, particularly when you say things like this:

> *Selfishness isn't simply a social term, it is a term that describes the outcome of an encounter with another entity. The development of the genes is NOT selfish, but in the vast majority of cases concludes with them doing what they do (self-interest) and in most encounters, they behave cooperatively or indifferently.*

That is not what the scientific issue is here. There are two major scientific issues I highlighted in my post, both of which are more concrete than non-specific claims about selfish vs. self-interested.

Issue 1 is genic selection vs. individual selection: There are specific predictions here: in the case of genic selection, the argument is that you can calculate the average fitness of an allele over all genetic backgrounds and make predictions about the impact of natural selection on that allele. Critics of the gene's eye view argue that this doesn't always work so well, such as in the case of overdominance.

Issue 2 is kin selection: again, you can make very specific predictions by calculating relatedness and the fitness cost of 'altruistic' acts (like worker bees not laying eggs). The more closely related two organisms are, the larger the fitness cost one should be willing to bear on behalf of the other – that's the prediction. And it's formulated rigorously – it's not hard to calculate relatedness of say, a worker bee to the queen.
Nature has helped us out by devising many different experiments – situations where you have societies of organisms – insects, birds, naked mole rats, etc. with different levels of relatedness. Kin selection theory makes concrete, *specific* predictions, and time and again, they are verified.

So this simply isn't true:

As near as I can find, there have been few actual experiments to confirm kin other than the higher probability that animals in the same geographic area will be related.

One example is the bee paper I cited – that work is done with experimental strains, where the researcher do know the extent of relatedness. And good field studies are also able to determine kin relationships.

As for Dawkins being ambivalent about his title, here is his intro to the 30th anniversary edition:

"Let me begin with some second thoughts about the title... Emphasize 'selfish' and you will think the book is about selfishness, whereas, if anything, it devotes more attention to altruism."

Here he makes more comments about the title:

> *I want to say a little bit, which I actually also said in the new preface to the 30th anniversary edition, so I won't spend long on it — about the title The Selfish Gene. I don't think it's a great title. I'm quite pleased with some of my other titles, but I don't think this is one of my best. It can — it has — given rise to misunderstanding.*
>
> *The best way to explain it is by correctly locating the emphasis. If you emphasize "selfish," then you will think the book is about selfishness. But it isn't, it's mostly about altruism. The correct word of the title to stress is "gene," and that's not because I ever thought that genes are deterministic in the sense that is politically objectionable to some people; it's because of a debate within Darwinism...*
>
> *Alternative titles could well have been The Immortal Gene, The Altruistic Vehicle, or indeed The Cooperative Gene. The book could equally well have been called The Cooperative Gene, and it would scarcely have needed to be changed at all.*

—
Mike

Link **Michael White** | 07/10/09 | 21:26 PM

> *...a theory (kin selection) that predicts that, in many cases, natural selection will favor altruistic behavior towards kin, and we have a definite locus that does in fact confer altruistic behavior – a*

> *region of DNA that contains a variant of a gene that causes female workers to cease laying eggs in the presence of a fecund queen.*

That's not an experiment for kin selection. The deck is stacked since ALL the animals are kin, so there can be no reliable prediction for altruism or anything else based on kin selection. The experiment I sited indicates that familiarity produced more positive results than kin, because the only way kin selection can be demonstrated is if the behavior is analyzed when the animals don't know that they are kin. Otherwise you can't differentiate kin from familiars.

In addition, while there may be a gene for altruism, there is no relation to kin selection, since many established bee colonies will accept a newly mated queen that has no genetic relationship to the hive at all. Therefore, if kin selection were playing a role, then the workers should recognize that this newly introduced queen is not related and begin competing with egg-laying activities to establish a new genetically linked colony. But this isn't what happens. Sometimes the workers will kill the newly introduced queen, but more often than not, the workers will accept the pheremone scent of the new queen (if the old one is gone) and continue without regard for kin relationship.

http://www.beemaster.com/site/honeybee/qpage.htm
http://www.indiansummerhoneyfarm.com/Introducing_Queens.htm
http://www.ehow.com/how_1739_re-queen-hive.html

In fact what we see is that the "altruism" is effectively hard-wired into the bees, so that they will behave in response to the hive conditions and can be fooled into accepting a queen that has no genetic relationship to them. This actually creates a stronger argument for group selection than it does for genes (in the eusocial insects).

I am glad to see that Dawkin's has backed off his earlier statements, but the quote I used was from his web-site, so apparently the word hasn't actually filtered down yet. However, it does appear from his comments that cooperation and even altruism may be more the rule than the exception. In other words, perhaps people can stop making the assumption that "selfishness" is the default position?

Regarding the unit of selection Futuyma also said *"...natural selection, which is a much more consistent, predictable, dependable change in the proportion of one gene vs. another, one genotype vs. another. Why? Simply because there is some consistent superiority, shall we way, of one genotype vs. another in some feature that affects its survival or some feature affecting its reproductive capabilities." (http://www.actionbioscience.org/evolution/futuyma.html)*

While there is no question that genes will dictate when form the organism takes and the traits that it possesses, it appears that this statement by Futuyma attributes the change in the genotype as possessing a feature that will affect an organism's survival or reproductive capabilities. That sounds like individual selection to me.

Now one could certainly argue about details and split hairs endlessly in this, but at the end of the day, the genes are along for the ride when it comes to sexual selection. If the genes convey some advantage (in survival or reproduction), then I don't think there's any question that they are playing a pivotal role in the survival of the organism. I'm simply saying that it's a stretch to argue that it is the gene that becomes the unit of selection. In an average of genetic traits, if a gene can raise the "average" of fitness, then you could make that claim, but I don't see it as a consistent argument. I'm also not suggesting that group selection is the criteria, since there may be influences there, but I don't believe they are sufficient in most cases to have large scale effects.

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Mundus vult decipi

Link **Gerhard Adam** | 07/10/09 | 23:27 PM

Mike, you said I only speak in vague generalities. I could not have been more specific when I criticised the godfather of selfish gene theory in **WD Hamilton, Selfish Herds, and other Biological Oddities**, an article that seems to have escaped your notice. I'm sure you'll address its specifics now you're aware of it.

Here's a specific, from your article. *"Bottom line: there are clear examples of 'selfish' genetic elements, with no positive fitness contribution, and which exist simply by virtue of the fact that they can perpetuate themselves."* That is not evidence for a theory of selfish genes as promoted by the gene-centrics, for as you stated *"Actually, their potentially negative phenotypic consequences are kept to a minimum by active surveillance and suppression."* They are controlled by the cell, their contribution to evolution is negligible.

Here's another specific from your article. *"The most controversial aspect of Dawkins' selfish gene argument is related to altruism."*
No, that's just one controversial aspect among many. In my mind it's the least controversial as its so easy to discredit, as Gerhard Adam has done.

The two crucial aspects of selfish gene theory that I see, are the claims that genes are independent units, and that they self-replicate, as seen in these quotes from the final chapter of the 30th anniversary edition of The Selfish Gene, the edition that you have quoted.
"...we have the beguiling image of independent DNA replicators, skipping like chamois, free and untrammeled down

the generations …immortal coils shuffling off an endless succession of mortal ones as they forge towards their separate eternities."
And this; *"Let me end with a brief manifesto, a summary of the entire selfish gene/extended phenotype view of life. …The fundamental unit, the prime mover of all life, is the replicator….Once a replicator has come into existence it is capable of generating an indefinitely large set of copies of itself. No copying process is perfect however, and the population of replicators comes to include varieties that differ from one another. Some of these varieties turn out to have lost the power of self-replication and their kind ceases to exist….As time goes by the world becomes filled with the most powerful and ingenious replicators."* (God, I love summaries!)

I'll deal with both of these fallacies together. Keep in mind that the assumptions they contain lie at the heart of selfish gene theory, because it's not a theory about segregation distorters, or "selfish" genetic elements that Dawkins admits are uncommon, or altruism, as you seem to be suggesting, it's a view of evolution itself.

DNA is not independent. It is a wholly dependent cog in a machine. When prompted by other genes it synthesizes a protein. That's it, end of story. Even that simple function then becomes subject to other gene inputs and cellular processes, so its phenotypic effects are far from certain. We could possibly attribute a degree of independence if self-replication occurred, but DNA cannot replicate itself. Gene replication is a function of the cell, not the separate genes doing their own thing. What I've described here is the situation for normal healthy organisms, the survivors of the process of natural selection.

Dawkins states as you've seen, that the selfish gene view is a view of life, but the selfish gene is a figment of the imagination. A cog in a machine cannot even be the explanation of evolution, let alone life itself.

The argument appears complex but is actually quite simple.
Selfish gene theory has attributed to genes a significance far in excess of that which exists in reality, for the reasons given.

Link **Steve Davis** | 07/12/09 | 02:04 AM

You're confusing the selfish DNA hypothesis with the selfish gene theory. Former refers to the fact that some DNA is (temporarily) neutral yet still gets copied or transcribed, while the latter refers to a theory which treats genes as competitive units.

LE Orgel and Francis Crick quote shouldn't be in here, even if their article occurred at a time when the selfish gene theory was gaining ground.

Link Anonymous (not verified) | 09/20/10 | 09:38 AM

I've had many a restless night wondering whether we are just lumbering shells to protect and reproduce genes, that there is no purpose to our existence and that anything is "allowed." But there was a part of me that knew I wouldn't feel guilty or that humanity wouldn't have so many psychological problems if survival of the individual's genes were all that mattered.

Then I found Jeremy Griffith. www.worldtransformation.com

Alex

Link Alex Owens (not verified) | 11/14/10 | 20:27 PM