I've been putting the case for some months now, that evolutionary biology is in a deplorable state due to an uncritical acceptance of the unrealistic assumptions that lie at the heart of selfish gene theory, by those who are directing current research. (See also Gerhard Adam’s articles on Hamilton’s Rule, Selfish Gene Theory, and Biology.) Contributing biologists have responded by telling me that my fears are groundless, that biology has moved on, that the influence of selfish gene theory has waned, that I should concentrate on the current literature and not dwell on the past. So I went to the trouble of checking out the Oxford University Zoology Department’s very good selection of papers available online, that deal with current research in this area.

There is indeed some excellent research taking place, but all the papers I've examined confirm my fears. The current research is taking place within boundaries established by selfish gene theorists three to four decades ago, and the conclusions drawn from the practical work conform to selfish gene theory.

Before we look at the current work, I'll just demonstrate the "long reach of the theory," a very long reach indeed. Included in the papers at the site is one titled "Altruism – A Quick Guide" by West Gardner and Griffin. Not only is their explanation of altruism a parroting of questionable concepts formulated forty years ago, we find at the end a section titled 'Where Can I find Out More?' And of the six references provided, the first is to "The Selfish Gene" (1976) and the third is to Hamilton’s 1964 paper. So much for biology moving on. (Hamilton, by the way, had not a clue about the scientific method, or if he did, he treated it with contempt. Check out his Geometry for the Selfish Herd, you’ll see what I mean.)

There’s a paper at the site by West El Mouden and Gardner titled “Social evolution theory and its application to the evolution of cooperation in humans” that is useful in showing the current state of evolutionary biology theory. The authors begin with

"There is considerable conceptual overlap between the fields of economics and evolutionary biology... Our overall aim in this paper is to provide an overview of evolutionary work on cooperation, in a way that is accessible to economists and other social scientists, emphasising common misconceptions."
The paper has been recently submitted to an economics journal in an attempt to clear up confusions that have arisen as a result of economists drawing faulty conclusions from evolutionary biology. A worthy project. But from what source does the confusion arise?

Let’s see what they present. (I’m quoting those sections I find problematic. Some sections are very good, such as their emphasis on the significance of cooperation at all levels of the natural world, and their advice that biological data should be given more weight than mathematical modeling. But it shows what a state the field is in, that such advice needs to be given.)

“Darwin’s theory of natural selection explains both the process and the purpose of adaptation … The duality of process and purpose in evolution is captured in Darwin’s suggestion that “natural selection can act only through and for the good of each being” (Darwin, Charles 1859).

These ideas were later formalised in mathematical terms by Fisher (Fisher, R A 1930;1941), who united Darwinism with Mendelian genetics, and described natural selection in terms of changes in gene frequencies. Specifically, Fisher showed that genes that are associated with greater individual fitness are predicted to increase in frequency, and hence the direct action of natural selection leads to an increase in the mean fitness of the population. This result is termed the ‘fundamental theorem of natural selection’, and was intended to capture the process (natural selection) and the purpose (maximisation of individual fitness) of adaptation.” (Emphases added)

Can you see the problem here? There is no purpose to adaptation, or at least, to adaptation that is genetic in origin. There is also no purpose to evolution, although “purpose” is indicated by that passage.

Confusion reigns.

They continued;

“Fisher’s theorem was frequently misunderstood in the population genetics literature prior to the late 1980’s (reviewed by Grafen, A 2003;2007c), and confusion still persists in the economics literature today (e.g. (Weibull, J W 1995). The first misunderstanding was the that fundamental theorem purports to describe total evolutionary change – it does not, and instead focuses upon the partial change in mean fitness, due to changes in gene frequency, that can be ascribed to the direct action of natural selection, neglecting other non-selective effects that are collectively termed ‘deterioration of the environment’ (Edwards, A W F 1994;Ewens, W J 1989;Fisher, R A 1930;Frank, S A and M Slatkin 1992;Grafen, A 2003;2007c;Lessard, S 1997;Price, G R 1972). The second misunderstanding was that the fundamental theorem concerns population fitness – it does not, and instead describes changes in individual fitness, which is expressed relative to the rest of the population.”

If “natural selection leads to an increase in the mean fitness of the population” and that “This result is termed the ‘fundamental theorem of natural selection’ then surely the theorem is concerned with population fitness! Economists have every right to be confused.

Let’s go on.

“Since Darwin, the only fundamental change in our understanding of how natural selection works has been Hamilton’s (Hamilton, W.D. 1964) development of inclusive fitness theory. (That’s a backward fundamental change as we’ll see.) The traditional Darwinian view struggled to explain many cooperative social behaviours, Fisher (1930) realised that genes can spread not only through their impact on their own direct transmission (direct fitness), but also through their impact on the transmission of copies of the same allele in other individuals (indirect fitness; see also Darwin 1859, pp 257–259), but he explicitly chose to neglect the latter effects in his derivation of the fundamental theorem. Hamilton (Hamilton, W.D. 1964) incorporated indirect fitness effects into a genetic theory of social evolution, and showed that the characters favoured by natural selection are those which improve the individual’s ‘inclusive fitness’, which is the sum of its direct and indirect fitness. The easiest and most common way in which indirect fitness benefits can occur is through helping close relatives, in which case genes are identical by descent (i.e. from a common ancestor), and so this process is usually referred to as ‘kin selection’ (Maynard Smith, J 1964)”

The crucial point here is found in; “The easiest and most common way in which indirect fitness development, raising question about use of anti-seizure drug

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benefits can occur is through helping close relatives,” For “indirect fitness” substitute “cooperation” and we see the obvious rebuttal of the accepted view of kin altruism. We cooperate with kin because they are closest to us. It’s easier to cooperate with someone living a few yards away, or who we see more often, than it is to cooperate with a stranger several suburbs or valleys away. (Or metres if you’re a microbe.)

Kin altruism has little to do with relatedness or identical genes, but it has plenty to do with distance. (Close physical distance that is.) And there’s a huge gap in understanding expressed in that quote. We (organisms) do not cooperate with kin to promote our genes. We (organisms) cooperate with kin to survive. We (organisms) also cooperate with unrelated organisms to survive. So our cooperative behaviours are not based on gene promotion; gene promotion is a by-product, an accidental outcome of one variety of cooperation. We cooperate to survive, and it’s this misunderstanding that explains the chasm that exists between selfish gene theory and reality.

They continued;

“Before describing the mechanisms that can explain cooperation, a general point about the differences between evolutionary mechanisms and rational choice theory is that evolutionary mechanisms only explain the average consequences of a behaviour. Therefore it is quite normal in nature to observe seemingly ‘irrational’ behaviour where an observed cooperative behaviour provides no direct or indirect fitness benefit, such as when a female gorilla protects human children that fall into her pen, when dolphins help an exhausted swimmer, or when enslaved ants rear the brood of the slave making species that captured them. However, these ‘irrational’ or seemingly maladaptive behaviours can be trivially explained by considering the average fitness consequences of such an evolved “rule-of-thumb”. Specifically, the underlying mechanism that leads to such behaviours will have only been selected for if they, on average, provide a direct or indirect fitness benefit. For example, the behaviour of the female gorilla may be a consequence of selection for maternal care, the behaviour of dolphins may be a by product of selection for helping within dolphin groups, and the rearing behaviour of the enslaved ants is favoured because it is usually directed towards related brood.”

They couldn’t help themselves could they? Here we have the inevitable drift into fantasy that we always see in those held captive by selfish gene theory. Do they really think that a gorilla cannot tell a human from a gorilla, that there is no larger motivation involved? Do they really think that a dolphin cannot tell a human from a dolphin, that there is not some larger motivation involved? A fact that cannot be explained by orthodox theory is that organisms have an affinity with other life forms. We humans for example, like to keep pets, to have gardens, to keep potted plants in our homes. We teach our children to read and write by using pictures of animals. We teach them to care for life by starting them off with pets that require little care. Prior to reading and writing becoming commonplace, we taught children moral values by way of fables featuring interactions between humans and animals. We nurture our bonds with other life forms. Do the authors really believe that a gorilla is incapable of similar motivation? There’s a serious problem here, of which more later.

A discussion of Hamilton’s rule and kin altruism followed, in which we find this;

“The first mechanism for generating sufficiently high relatedness to make indirect fitness benefits important is kin discrimination, when an individual can distinguish relatives from non-relatives and preferentially direct aid towards them (nepotism) (Hamilton, W.D. 1964)”

But why are indirect fitness benefits important? Cooperation between close kin is just a form of cooperation. It’s only important when pushing the line that genes are manipulating things behind the scenes, ensuring that identical genes are passed on.

They continued; “In Belding’s ground squirrels, individuals discriminate kin on the basis of odours from oral and dorsal glands (Mateo, J M 2002), and use alarm calls to preferentially warn closer relatives of the approach of predators, despite the fact that this increases their own visibility to predators (Sherman, P W 1977).”

Don’t you just love Belding’s ground squirrels? They provide such a great example of kin altruism and kin selection. There’s one small problem. More than one, actually. What the authors don’t tell us is that another ground squirrel inhabits the same terrain and range as the Belding’s; it also discriminates kin by odours, but does not engage in the same nepotistic behaviours. If kin
behaviours were as fundamental to evolution as the theorists would have us believe, they would be observed here as well. The simple fact is that kin altruism is secondary to general cooperation as a factor in natural selection. But we can’t talk of general cooperation can we? Because that does not fit the so-called “Darwinian” view of evolution. The other small problem is those alarm calls. Are we really expected to believe that a predator hears the call and understands its meaning, while unrelated squirrels are oblivious to what’s occurring?

We’re about 1/3rd through the paper and already we can draw some conclusions.

Evolutionary biology; it’s a great area to get into if you enjoy a good fantasy. Or if you fit Locke’s definition of a madman: “one who reasons correctly from incorrect premises”. Or if you fit N. N. Taleb’s description of investment portfolio managers: “they combine the technical expertise and lack of understanding that we see in idiot savants.” Those sound like cheap throwaway lines, but I use them with a certain cautious respect. Most of those who are pursuing these unrealistic conclusions have more brilliance in their little fingers than I have in my entirety, but their conclusions will always be off-target because they have not learned to analyse, to question, to challenge. As a result they are incapable of seeing the obvious. They live in a world awash with cooperation, yet they see selfishness everywhere. To them cooperation is a problem. (The phrase “the problem of cooperation” is littered throughout this paper and all others on the subject.)

It’s a problem because it does not fit in with accepted Darwinian theory. The trouble with accepted Darwinian theory is that Darwin would have had none of it. He made it quite clear in The Descent of Man that group cooperation is a factor in natural selection, and that social instincts are superior to, and in the long run dominate, individual instincts.

The fact that Darwin believed this, does not make it fact. But it’s fact just the same. So what we are dealing with here is not Darwinian theory at all, it’s Hamiltonian theory.

The paper makes little difference in regard to confusion over evolutionary biology, other than to add to the confusion. So what is the basic problem here?

Let me make it clear that the criticism that follows is not directed at the authors of this paper, but at the field in general. In fact, to give these authors credit, they disagree with the view that mutually beneficial behaviours among non-kin are “less interesting” than kin cooperation, but the fact that they have seen the widespread exclusion of non-kin cooperation as a mistake, serves to highlight the lack of analytical drive in this field.

The problem started when WD Hamilton took Fisher’s relatively uncontroversial view of natural selection and distorted it beyond recognition. (Fisher did however open the door for Hamilton, by depicting evolution as a mathematical process and describing evolution in terms of changes in gene frequencies.) He developed from it a genetic theory of social evolution so incorrectly focused that it had little connection to reality. The drift from reality occurred by focusing on indirect fitness benefits to explain kin altruism while pushing general cooperation to the sidelines.

Here’s an explanation of it;

“Hamilton’s inclusive fitness (kin selection) theory explains how altruistic cooperation can be favoured between relatives. This is encapsulated in a pleasingly simple form by Hamilton’s (Hamilton, W.D. 1963;1964;1970) rule, which states that a behaviour or trait will be favoured by selection, when rb-c>0, where c is the fitness cost to the actor, b is the fitness benefit to the recipient, and r is their genetic relatedness.”

For a start, there is no reason to assume, on the basis of an equation comprised entirely of variables and from which no definite outcomes can be determined, that the process described is of primary significance in social evolution. I’m not denying that kin altruism assists survival. I’m not denying that kin altruism promotes genes that are identical by descent. But kin altruism is merely a behaviour that falls under the category of general cooperation. Why would Hamilton push such a misleading line?

The answer to the confusion lies in the term “inclusive fitness”. Inclusive fitness is the sum of direct and indirect fitness benefits. Direct fitness refers to a particular individual, but indirect fitness, Fisher’s secondary concept pushed to the forefront by Hamilton, refers to benefits that are said to occur when genes identical by descent are promoted in one individual by another individual. Can you see the problem that’s developing? What’s happened here is that the concept of inclusive fitness has
been tailored by Hamilton to give validity to selfish gene theory. To give genes a greater significance in the process of natural selection than actually occurs. Fitness has always been taken to mean the survival and reproductive success of an individual. But here it means something altogether different; the success of identical genes. The focus has been taken from the organism, the level at which natural selection is acting, and the spotlight put squarely on genes.

Fisher stated that gene frequencies change through the action of natural selection, nothing wrong with that. Hamilton turned Fisher’s position on its head to state that a change in gene frequency is a form of selection. (Kin selection.) Big mistake! Suddenly we’ve gone from “natural selection causes changes in gene frequency” to “a change in gene frequency is selection”. He has mistaken an outcome as the process. A change in gene frequency is merely a result of natural selection, as Fisher well knew. By defining selection as gene promotion, instead of following Fisher’s legitimate line of describing an aspect of evolution in terms of changes in gene frequency, Hamilton was able to create the illusion that natural selection is all about genes.

That illusion has befuddled biologists ever since. (Don’t forget that although Fisher came up with the concept of inclusive fitness, he “explicitly chose to neglect the latter effects (indirect fitness effects) in his derivation of the fundamental theorem.” Smart man.) As a result we see ridiculous claims accepted as orthodoxy, such as the mistaken view above, that the only important cooperation is among kin, or that only genes can be considered as the beneficiaries of cooperation, or one of my favourites; that altruism can only spread by kin selection. Total madness. Brilliant reasoning based on false premises. Technical skill combined with a lack of understanding.

What are the fallacies of Hamilton’s view of evolution? There are many, but to avoid repetition from previous articles we’ll only consider those that came from this discussion.

First, direct fitness as described by Hamilton is a biased concept as it ignores the contribution to an individual’s fitness made by non-kin cooperation.

Second, Hamilton’s indirect fitness concept is flawed because it relies on the incorrect assumption that genes have fitness. Genes do not have a fitness factor because fitness only applies to entities that reproduce themselves. An organism produces another organism, but a gene does not produce another gene, let alone an identical copy of itself, as is implied. Gene production is a function of the cell.

This means that inclusive fitness theory as described by Hamilton is not an explanation of the evolution of social behaviours as he claimed. His inclusive fitness theory is baseless. (If you’re not convinced by the idiot savant analogy, check out Hamilton’s inclusive fitness paper.) Kin altruism does promote genes that are identical by descent, but my question is, so what? Kin altruism is just a category of kin cooperation which is merely a category of general cooperation. Hamilton’s concept of indirect fitness is misnamed and merely describes the process by which genes identical by descent are promoted, which might be of interest with regard to certain questions, but which is far from being an explanation of social evolution.

The study of gene frequencies that has flowed from this misperception is merely a study of statistics. It is not a study of evolution because genes are not isolated entities. It is not genes that are evolving, it is organisms and groups. As previously discussed, genes do not reproduce themselves, the image of “immortal replicators” is therefore a fallacy, but the significance of this is far greater, and it cuts to the heart of the Hamiltonian view of evolution. Not only are genes incapable of reproducing, they are incapable of independent action in any sense. All gene functions are controlled by the cell, so any explanation of evolution that focuses on genes and ignores cell functions will be flawed.

So if genes are not the driving force of evolution, or the story of life itself as the gene–centrics would have us believe, then what is going on when an insect is born, struggles to reproduce, then dies within a few hours? Or when young parents proudly show their new–born baby to family and friends? They are not proud because they have advanced their genes; they are proud because they have created life. Life begets life, as with the insect during its short existence. It’s that principle that explains our affinity with other forms of life. It’s that principle that solves “the problem” of cooperation.

So I must concede that the West El Mouden Gardner paper has made a little progress. The authors at least recognise that Hamilton’s view of evolution was deficient as it ignored general cooperation. But their handling of this tells us a good deal about the current state of evolutionary biology. There was not a word of criticism of Hamilton’s inclusive fitness theory.
Can’t hold a sacred text up for scrutiny, can we? Until the theorists break free from Hamilton’s iron grasp, they will continue to flounder.

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COMMENTS

You really are a gadfly this time! As always, I think you are a brilliant writer and, as always, I think you are basically being a friend to evolutionary biology. But that title is going to get some attention so I hope you thought it through – few people who devote their lives trying to understand the mysteries of science (for peanuts) find something positive about having the word ‘idiot’ in the title of an article about their work.

Reply to This » Link  Hank Campbell | 09/19/09 11:05 AM

That’s a fair criticism Hank, and one that probably needed to be made to clear the air. But anyone feeling offended by the title should put the “idiot” to one side and focus on the “technical skill combined with a lack of understanding” side of it. There’s no point in shooting the messenger, the fact is that Hamilton’s bogus treatment of inclusive fitness should never have become the foundation of evolutionary theory.

And I did not take on this project to make friends, but happily that has happened, for which I’m grateful.

Reply to This » Link  Steve Davis | 09/19/09 14:04 PM

... rb-c>0, where c is the fitness cost to the actor, b is the fitness benefit to the recipient, and r is their genetic relatedness

The problem with that equation is that it unequivocally states that if there is no genetic relatedness then a fitness cost should never be incurred by the actor. So the first explanation that has to occur is how this equation relates to the introduction of a new, unrelated honeybee queen to an existing hive where no genetic relatedness exists. In this scenario, the equation predicts that the workers should all abandon the new queen and compete to producing their own genetically-related queen. Since every beekeeper knows that this doesn’t have to occur, it definitely makes the equation’s validity suspect.

More to the point, I have never seen a reliable means of expressing or determining the costs or benefits (nor how probabilities for either) should fit into the calculation.

Reply to This » Link  Gerhard Adam | 09/19/09 14:06 PM

You’re right Gerhard, and I suspect it was that equation that tipped the balance in having inclusive fitness theory accepted.

Reply to This » Link  Steve Davis | 09/19/09 14:16 PM

Another thing just struck me. Once an animal has reproduced all it’s going to do (i.e. old age), then the cost goes to zero. This would result in virtually unbridled altruism towards unrelated animals since there...
is no cost to any action that would decrease the actor's fitness (since it has already been maximized).