

Re: Perpetually Perplexed

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Joe Felsenstein wrote:–

> >> *GH:–*
> >> *Yes. Let me try to be more precise about the meaning of*
> >> *Hamilton's Rule*
> >> *that I implied here. If you take the Rule to indicate that a mutation*
> >> *creating an altruism allele will tend to selectively increase*
> >> *in frequency,*
> >> *then I am arguing that the dispensing of altruism is assumed*
> >> *to be perfectly*
> >> *graded. To the extent that the grading of altruism with kinship is not*
> >> *perfect, then too much personal fitness is lost through*
> >> *altruism toward more*
> >> *distant relatives and/or too little inclusive fitness is lost*
> >> *by failing to*
> >> *be optimally altruistic toward closer relatives. Whatever the*
> >> *suboptimal*
> >> *mix, the conditions for selective frequency increase would be*
> >> *more stringent*
> >> *than indicated by Hamilton's Rule.*

> > *JM:–*
> > *Edser has occasionally written to the effect that there is a herd*
> > *behavior among professional biologists in which they will not attack*
> > *one of their own, but will cooperate in defense against outsiders.*
> > *I am going to succumb to the temptation to give no response to your*
> > *post and see what happens. You have provided an excellent opportunity*
> > *for refuting John's hypothesis.*
> > *I will also follow Edser's lead and explicitly challenge Joe Felsenstein*
> > *on this.*

> *JF:–*
> *OK, yes, I disagree with Guy. Hamilton's argument uses the quantity*
> *r for the average degree of relationship between the altruist and the*
> *recipients.*

JE:–

The "average degree of relationship between the altruist and the recipients" is not sufficient to calculate any one *_specific_* comparison of rb with c , just a population average of such comparisons within which all specific selective action is lost. Since relatedness forms a major component of Hamilton's incomplete fitness total rb it must be measured specifically for each comparison of rb with c and not just generally over many comparisons via a mean value of r .

> *JF*:–

- > *The altruist can be simply being nice to the neighbors,*
- > *who happen to partly be its relatives.*

JE:–

The selective motivation for such behaviour can be mutualistic OR altruistic. In fact, it is predicted that mutualism (which requires no altruism via proxy reproduction) can more easily evolve within families and extended families simply because they are more likely to remain in close contact with each other. In the eusocials, mammals or insect, this closeness along with a pheromonal control of offspring fertility via enclosed nest spaces allowed fertile parents to be selected to maintain an army of sterile offspring to act as slaves to their own parents. Once again no Darwinian altruism was involved. Mutualism between fertile parents allowed genes to be selected and passed to offspring that maintained most of these in a sterile state. Sterile offspring act as modular body parts to their parents. Hamilton et al maintain an opposing causative theory. Offspring sterility evolved via selection operating at an independent gene level of selection within the bodies of sterile forms forcing these forms to 100% donate their own fitness to their parents. One key observation that may separate these contesting theories is any documented observation in nature of the reproduction of a fully fertile form that never normally reproduces itself becoming sterile and remaining sterile until it dies of old age. Does Dr Hunt have such a documented

example within the eusocials?

Most illustrations of 0.5 IBD relatedness using Hamilton's Rule incorrectly employ Haldane's Pub rule where the recipients are helped directly. Here b would represent the number of recipients helped. In Hamilton's Rule b helps the offspring of these recipients which is one more generation removed. This means the maximum relatedness IBD can be for any reproduction by proxy using Hamilton's Rule is 0.25 and not 0.5. Within Hamilton's Rule all maximal 0.5 relatedness must refer to each parents specific relatedness to just their own offspring which is not a mean gene relatedness but not a mean organism relatedness. Normal reproduction is not altruistic and provides no proxy wastage. Felsenstein (below) calculates an example of this enormous wastage which must be paid by every proxy reproductive act, i.e. every time relatedness < 0.5 within Hamilton's Rule (the maximal organism specific IBD relatedness possible using normal sex).

> *JF*:–

> *If, say, the neighbors were*

> *half of them first cousins of the altruist then the appropriate*

> *value of r is $(1/2) \times (1/16)$ where $1/16$ is the r value for cousins.*

> *This adjustment of r (the factor of $1/2$) above takes care of the*

> *dispensing of altruism to some non-relatives.*

JE:–

This value of " $1/2$ " only constitutes a needless waste that is not evident if the parents normally reproduce because all of your own offspring are related 0.5 to yourself with normal sex producing no such waste. Helping 16 cousins where you cannot tell what their relatedness is to you, so you needlessly waste your finite resources helping (most probably, Hamilton's competitive wildtype non altruistic allele!) cannot compete against helping just 2 of your own reproductives related 0.5 because you save the " $1/2$ " within Felsenstein's $(1/2) \times (1/16)$ calculation, i.e. a massive "buy one and get one free" 50% saving..

> *JF*:–

> *There is no assumption in Hamilton's work that the altruist recognizes*

> *kin. This is a common misconception about the kin selection argument.*

JE:–

Why doesn't Felsenstein explain why it remains an absolute necessity that the altruist cannot recognize the kin?

When the same genomes seek each other out to mate to just linearly reduce Felsenstein's needless 50% waste (indicated by the "1/2" within $(1/2) \times (1/16)$ above) they suddenly rediscover the geometric cost of previously deleted epistasis. The best known example is Dawkins Green Beard model which still remains accepted within the literature. The gains of such non random sexual selection (Hamilton only specified random mating) are always less than the geometric rising cost of previously mathematically deleted epistasis:

$$(r^e)b > c$$

where e is the number of independent epistatic loci that code for the organism altruistic phenotype. For Dawkins Green Beard model e=2. This e value represents just the minimal cost of epistasis yet it provides the reason as to why the rule fails. I have been posting this for over a year. Felsenstein even thanked me for it. However NAS, EK, BOH etc continue to just ignore it.

Hamilton's mathematical deletion of genetic epistasis by only using $r=1$ remains fatal to Hamilton's Rule because Hamilton's selfish allele cannot have any lineal i.e. INDEPENDENT fitness without it. When you set $r = 1$ it remains "gone but not forgotten".

In a sense, Hamilton's organism altruism gene is addicted to $e = 1$ because without it his selfish gene is forced to have a DEPENDENT fitness at Darwin's organism level. In this situation forcing organism altruism must reduce selfish gene fitness as well as organism fitness so it cannot be selected for.

Allowing $e=1$ removes fitness dependency at the cost of every gene within one genome now being forced to compete against every other at Hamilton's heuristic independent genome level of selection. Now one Darwinian organism fitness must be the simple sum of the fitness of each independent gene fitness within one genome. Such an event has never been documented in nature because it remains biologically absurd. In fact not one single linear gene fitness has ever been documented within nature. Yet, Hamilton et al see fit to assign such a fitness to their selfish gene. Hamilton's organism altruistic gene is damned if it does and damned if it doesn't.

Relatedness always remains:

$$r^e$$

where $e=1$ using Hamilton's simplification of e was allowed by Fisher. Only by deleting all epistasis in this way can Hamilton create for himself his own heuristic (dare I say it "Mad Hatter") world within which altruism CAN evolve but by only supposing a genome composed of just one locus with two alleles. This is because only this massively simplified selectee allows one gene to become equivalent to one Darwinian individual. As soon as you make it more real by adding just one more locus, unless these alleles always freely compete against each other within Hamilton's genomic level (which in turn must compete against Darwin's single Darwinian fertile organism level of selection) they cannot become kin selected because kin selecting 2 or more genes reduces r^e geometrically so rb cannot compete with c (non kin selection).

In order to keep all these genomic genes freely competing instead of only tightly cooperating to produce just THE ONE Darwinian fitness total at a higher fitness level all genetic epistasis must remain deleted.

The amazing thing is rb does not care a less about the organism phenotypic and

its fitness, it only cares about a better 100% relative way to reproduce, on just a gene by gene basis, *ANY* gene. The fact that these genes have a real phenotypic fitness remains central to Darwinism but is simply deleted by Hamilton et al. In Darwinism reproducing genes becomes an effect of another cause: selection acting by comparing each parents total Darwinian fitness within one population. In Hamiltonian reasoning the reproduction of genes over organism generations now becomes the selected cause so that any Darwinian phenotypic fitness is just reduced to an effect of this new cause, i.e. cause and effect were allowed to be entirely reversed within Hamilton's heuristic model.

In the Darwinian view genes can only be selected to promote organism reproduction but within the Hamiltonian view organisms are only selected to promote gene replication note however: over just organism and not gene generations. Both cannot be correct can they! Is this why Prof. Felsenstein still refuses to discuss cause and effect within the biological sciences?

My most sincere regards,

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