

# Re: Hamilton's rule

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- *From:* "Perplexed in Peoria" <[jimmenegay@xxxxxxxxxxxxxx](mailto:jimmenegay@xxxxxxxxxxxxxx)>
  - *Date:* Thu, 17 Nov 2005 15:58:19 -0500 (EST)
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"Guy Hoelzer" <[hoelzer@xxxxxxx](mailto:hoelzer@xxxxxxx)> wrote in message [news:dlh6sj\\$274\\$1@xxxxxxxxxxxxxxxxxxxxxxxxxxxx](mailto:news:dlh6sj$274$1@xxxxxxxxxxxxxxxxxxxxxxxxxxxx)  
> in article [dft8t\\$2fog\\$1@xxxxxxxxxxxxxxxxxxxxxxxx](mailto:dft8t$2fog$1@xxxxxxxxxxxxxxxxxxxxxxxx), Perplexed in Peoria at  
> [jimmenegay@xxxxxxxxxxxxxx](mailto:jimmenegay@xxxxxxxxxxxxxx) wrote on 11/16/05 10:20 AM:  
>  
>> "Guy Hoelzer" <[hoelzer@xxxxxxx](mailto:hoelzer@xxxxxxx)> wrote in message  
>> [news:dldgfc\\$1drk\\$1@xxxxxxxxxxxxxxxxxxxxxxxxxxxx](mailto:news:dldgfc$1drk$1@xxxxxxxxxxxxxxxxxxxxxxxxxxxx)  
>>> in article [d158qa\\$p8l\\$1@xxxxxxxxxxxxxxxxxxxxxxxx](mailto:d158qa$p8l$1@xxxxxxxxxxxxxxxxxxxxxxxx), Catherine Woodgold at  
>>> [an588@xxxxxxxxxxxxxxxxxxxx](mailto:an588@xxxxxxxxxxxxxxxxxxxx) wrote on 11/12/05 9:29 AM:  
>>>  
>>>> Guy Hoelzer ([hoelzer@xxxxxxx](mailto:hoelzer@xxxxxxx)) writes:  
>>>>> My confusion is rearing its ugly head again. If the axes of the graph are  
>>>>> "frequency in focal individual (Y axis) vs frequency in population (X  
>>>>> axis)", then I don't see how dominance/recessiveness can influence the  
>>>>> lines  
>>>>> at all. What am I missing?  
>>>>  
>>>> One of the lines is labelled "donor". The only individuals  
>>>> who act out the "donor" phenotype are the ones which have  
>>>> the set of genes that code for altruism. If altruism is  
>>>> a recessive trait, then all of the "donors" must have  
>>>> two copies of the altruism gene. Therefore the frequency  
>>>> in the "donor" focal individual is always 1 if altruism  
>>>> is a recessive trait.  
>>>>  
>>>> But if the altruism gene  
>>>> is dominant, then the set of "donors" includes some  
>>>> individuals with one copy of the gene and some individuals  
>>>> with two copies of the gene. If an individual is  
>>>> observed to carry out an altruistic act, or if it  
>>>> finds itself experiencing an overwhelming urge to  
>>>> carry out an altruistic act, then an observer  
>>>> (or the organism itself) can conclude that the  
>>>> individual has one or two copies of the altruism gene.  
>>>> The expected frequency in this individual can thus be  
>>>> predicted to lie between 0.5 and 1 (closer to 1 if  
>>>> the altruism gene is very common in the population).  
>>>>  
>>>> Maybe I should have said more. All of this was apparent to me. In the

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>>> artificially restricted world of modeling perfect dominance/recessiveness  
>>> the starting point of the donor line would be 0.5 (pure recessiveness) or  
>>> 1.0 (pure dominance). In either case, however, there is a simple linear  
>>> relationship on the frequency/frequency graph that converges on the point  
>>> (1,1). The comment you quoted above came from a discussion where I thought  
>>> it was implied that the shape of the relationship (e.g., linearity) was said  
>>> to depend on dominance/recessiveness. I may have been reading too much into  
>>> Jim's comments, which I still think reached way outside the scope of the  
>>> simple frequency/frequency graph.

>>

>> Reached way outside how? My claims are fairly simple:

>> – If the (single) altruism locus is purely recessive, the graph of allele  
>> frequency in donors is a constant 1.0. (Obviously).

>> – If the altruism locus is purely dominant, the graph of allele frequency  
>> in donors rises linearly from 0.5 to 1.0 as the allele frequency in the  
>> population rises from 0.0 to 1.0. I am uninterested in a 'glitch' in  
>> this curve at allele frequency exactly 0.0 – there technically are no  
>> donors at exactly this frequency.

>

> I'm with you so far.

>

>> – Given other assumptions about gene expression besides pure dominance or  
>> recessiveness, it is possible that the donor line may be something other  
>> than linear. That doesn't matter as long as the donor D line never drops  
>> below the 45 degree population P line. Regardless of how the line runs,  
>> or of how many loci are involved, it remains the case that the recipient  
>> R line lies a fraction 'r' of the way up from the P line to the D line.  
>> This fact is a consequence of the definition of IBD 'r' and the assumption  
>> of random mating.

>

> Ooooooh. I got lost in semantics here. Let me try to put some words in  
> your mouth and you tell me how they taste. The R line does not represent  
> the frequency of the allele among actual recipients.

Well, it represents individuals related to the donor(s) by r. That pretty  
much means the same thing as 'recipients' to me.

> Instead, it represents the tipping point of HR. If the recipients of  
> altruism fall above the R  
> line relative to their donors, then HR predicts that kin selection will  
> favor the altruism allele.

No! The lines have been drawn without reference to the values of b and c.

> It would be optimal, from the viewpoint of the  
> allele, if actual recipients had the maximum number of altruism alleles  
> possible (2).

Yes, but if we are going to use Hamilton's rule, the expected number of  
copies of the allele will be  $(P + (D-P)r)$ ; that is, the expected number  
of copies in the recipient will be R. But sometimes the donor will be

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lucky and find 2 copies in the recipient. But sometimes he will be unlucky and find none. Actually the donor doesn't care that much. The recipient will have a similar excess of ALL of the donor's genes, not just the altruism allele. The donor is not trying to spread the altruism allele per se. He is 'trying' to spread ALL of his genes.

>> This fact is all that is needed to establish Hamilton's rule.

>

> I'm going to have to apologize again for being dense, but I don't see how > your graph justifies HR at all.

Well, the graph doesn't exactly justify HR. The relationship  $R = P + (D - P)r$  plus some simple reasoning justifies HR.

> It would be a nice graphical representation of the HR claim,

No it wouldn't. The graph says nothing about 'b' and 'c'.

> but how would it lead to the conclusion that the R line  
> ought to lie "a fraction 'r' of the way up from the P line to the D line."  
> This is essentially the claim of HR, ...

You are apparently working under the 'tipping point' misunderstanding that you tried to put into my mouth above. You are incorrect.

> but it seems to be something that you have assumed here.

Yes, I assumed it in drawing the graph. The graph reflects this assumption. But the assumption is easy to prove.

> As you said, "this fact is a consequence of the  
> definition of IBD 'r' and the assumption of random mating." Because it  
> relies so fundamentally on the definition of IBD 'r', how can it justify the  
> use of IBD 'r'?

You are beginning to sound like McGinn. The logic is that the definition of 'r' (IBD) and the assumption of random mating leads to the relationship  $R = P + (D - P)r$ . That relationship, leads (by a different line of reasoning) to Hamilton's rule. We use the IBD definition of 'r' because it leads to a nice (and correct) rule.

>> The rule does not depend on linearity. The frequency  
>> independence of the rule does not depend upon frequency.  
>  
> OK.

You have just said OK to a typo. I meant to write that the frequency independence of the rule does not depend upon the linearity of the D line and the R line.

>> – What MAY depend on frequency is how fast the altruism allele spreads.

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>> That will depend upon just how separated the lines are, and the count  
>> of altruists (or of acts of altruism, depending on what b and c measure).  
>> It will also depend on the size of b and c. I offered my straight lines  
>> as an argument against YOUR claim that the impetus toward the spread of  
>> the altruism alleles pretty much peters out at gene frequencies of 30–40%.  
>  
> Under your graphical model, which I accept as a representation of Hamilton's  
> model, the strength of kin selection diminishes monotonically with the  
> frequency of the allele.

Well, if you mean that the difference between the inclusive fitness of an altruist and the inclusive fitness of a member of the general population decreases monotonically, then yes.

> I guess you have swayed me to the position that  
> under Hamilton's model, as opposed to a more realistic version of the same  
> model, there is not a frequency threshold where kin selection becomes  
> irrelevant. Instead, it becomes irrelevant monotonically.

In the same way that any beneficial trait becomes irrelevant as more and more of the population has that trait.

But perhaps a better way to look at it is to compare the possessor of the trait to (not the population average, rather to) an individual without the trait. If you compare in this way, then I don't agree that the 'strength of kin selection' decreases monotonically. Once the allele becomes fixed in the population, there is still strong selection AGAINST mutations that change the altruism allele to selfishness (i.e. ineffectiveness).

>> So, I have to ask, what exactly are your claims? Do you still believe that  
>> the spread of kin-selected altruism peters out at this level, and that only  
>> reciprocity can take things further?

>  
> Well, I still believe that the strength of kin selection peters out as the  
> allele becomes more common. Your graphical model confirms that for me. I  
> also still think that the kin selection model is entangled with the  
> reciprocal altruism model, which I see as more general and a more plausible  
> explanation for most altruism in nature.

>  
>> If so, what kind of D and R curves  
>> are you postulating? And why do you think the curves have that shape?

>  
> I accept your explanations of D and R curves. Thanks for your patience.  
> :-)

>  
> Guy

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- **Follow-Ups:**
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- **References:**
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    - ◇ *From:* Catherine Woodgold
  - ◆ **Re: Hamilton's rule**
    - ◇ *From:* Guy Hoelzer
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    - ◇ *From:* Perplexed in Peoria
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